Invertebrate community structure along a habitat-patch size gradient within a bog pool complex

by

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Abstract

This thesis characterises species richness and community structure over a habitat-patch size gradient of a typical bog-pool complex, investigating the effect of pool size on aquatic invertebrate communities. In this study, twenty-two pools were surveyed ranging in area from 8.6 m^2 to 280.9 m^2 within a single complex at Forsinard in the north of Scotland. Three different sampling methods were used: baited and unbaited activity traps and a sediment sampler. Univariate and multivariate methods were used to investigate the effects of pool size and pool location within the complex on species richness and community structure.

The research expands our knowledge of peatland pool invertebrates by providing a comprehensive survey of the aquatic invertebrate fauna representative of the Flow Country of northern Scotland. Two IUCN British Red Data Book species were recorded: the Northern Damselfly, *Coenagrion hastulatum* (Charpentier), and the cased caddisfly, *Nemotaulius punctatolineatus* (Retzius). Three species of aquatic Coleoptera were collected that have Nationally Notable status according to Ball (1986): *Dytiscus lapponicus* Gyllenhal, *Ilybius aenescens* Thomson and *Gyrinus minutus* Fabricius. All these species are typical of, and often restricted to, this habitat type. The three different sampling methods differed in their sampling efficiency and each gave a different species spectrum. A distinct seasonal change in the samples was also observed.

The number of taxa caught per standardised sampling unit (taxon density) was investigated over the pool size gradient. Relationships between taxon density and area were weak or non-existent in both unbaited activity traps and sediment samples. However, the number of beetle species caught in baited activity traps increased significantly with pool size, indicating that the total number of beetle species per pool may also increase over the size gradient. Ratios of the number of predator taxa to prey (non-predator) taxa for each pool ranged from 0.34 to 0.78 with a mean of 0.49 and were not affected by pool area or total taxonomic richness. Taxa displayed a positive abundance-occupancy relationship and the possible underlying mechanisms involved in creating this pattern are discussed. Multivariate techniques showed that pool area, depth, and distance from the centre of the pool complex (periferality) all had a small but significant affect on community composition and that between certain taxa there were distinctly different optima along the pool size gradient. These results are discussed in the context of species area theory.

Declaration

This thesis has been composed by myself and the work it describes has been carried out by myself except where specific reference is made to other individuals.

Naomi M. Towers

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1 Introduction

1.1 POOL AREA AND INVERTEBRATE ASSEMBLAGES

It is a logical idea that a large area will support more individual organisms than a small area of equivalent habitat. As the number of individuals increases, the probability of the inclusion of new taxa increases thereby increasing species richness. Published statements on this matter date back to 1855 (see review by McGuinness, 1984a) and species-area curves, where the number of species observed increases as a function of area, were fitted to plant community data as early as 1859 (Rosenzweig, 1995). Species-area relationships have since been found in many other types of community such as amphipods in caves, (Culver, 1970), organisms in small bodies of water (Maguire, 1971) breeding birds on water-bound islands (Coleman *et al.*, 1982) and even in the fauna of intertidal boulders (McGuinness, 1984b)

Although the pattern of an increase in the number of species with an increase in area is clear, the mechanisms that create it are not (Connor & McCoy, 1979; McGuinness, 1984a; He & Legendre, 1996). More individual organisms will fit into a larger space but is an increase in space alone, and the subsequent increased probability of the addition of new species, responsible for an increase in the number of species present? MacArthur and Wilson (1963; 1967) proposed the theory of island biogeography which states that on small islands, due to a small target area, immigration rates are lower and that, due to small populations, extinction rates are higher, resulting in fewer species on the island. Large islands, with a large target area and large populations that are less prone to extinction, will support more

species. Also called the area *per se* hypothesis by Connor and McCoy (1979), area alone is the major factor explaining species richness. Area alone has been shown as the major factor driving an increase in species richness in several studies (e.g. Simberloff, 1976; Abbott, 1978; Boström & Nilsson, 1983; bat fauna in Ricklefs & Lovette, 1999).

An alternative mechanism proposed to explain the species-area relationship is an increase in habitat heterogeneity with an increase in area (Williams, 1943). Increased microhabitat diversity allows 'new' species to exploit an increased number of different niche spaces, resulting in greater species richness. Many studies have explained the areal increase in species richness by an increase in habitat diversity (e.g. Williams, 1943; Maguire, 1971; Douglas & Lake, 1994; Fox & Fox, 2000; see also Rosenzweig, 1995). Other explanations for the species area relationship have been proposed and are discussed elsewhere within this thesis.

Most studies of the effects of an increase in habitat patch or island area are concerned with the effect on the total number of species found. However, an increase in species richness does not tell us *which* species are being added. In addition to determining whether an increase in species richness takes place, it is interesting to ask how an increase in space alone affects community structure. If species of different functional groups or trophic levels are added disproportionately then, as species richness increases, the structure and functioning of a community may also change. Alternatively, even if species richness is not affected by area, this does not mean that the composition and structure of an assemblage remains unchanged. The interesting questions therefore are:

a) Does a system demonstrate a species-area relationship?

b) If so, are the additional species found in larger habitat patches selected at random from the pool of available species, or are there underlying ecological constraints on those which can colonise?

c) If no species-area relationship is apparent, are there nevertheless differences in community structure between small and large habitat patches and, if so, what is driving these differences?

The system used to test my hypotheses is an aquatic invertebrate assemblage within a bog pool complex in the Flow Country of northern Scotland. A series of 22 pools along a natural size-gradient were sampled. All pools were similar in water chemistry, depth (less than 1 m), nutrient levels, hydroperiod (all were permanent pools) and microhabitat diversity. Local environmental conditions such as climate, altitude and underlying geology did not differ. The only appreciable difference between the pools was their size, allowing me to test for differences in the invertebrate assemblages along a size gradient whilst keeping confounding factors to a minimum.

This project has an important application to many real systems. Pools can differ in size for many different reasons. In their natural state different pools obviously vary in size, but events such as drought or drainage and rechannelling of the water table can reduce pool size through time. The ecological significance of such a disturbance may be important to the aquatic invertebrate communities. In Scotland, afforestation for example, has lead to large areas of the peatland being drained and many bodies of standing water have reduced in size or disappeared altogether. With the exception of the beetle taxa, little is known about the invertebrate fauna of peatland pools, particularly in the Flow Country, and even less

is known of the effects of pool size. This thesis provides a detailed survey of the invertebrate fauna of a unique and little studied habitat type. The results record species not previously listed in the Flow Country (partly through lack of information available) and help explain invertebrate community structure within species-poor peatland pools.

Because I have been able to examine the effects of area unconfounded by other variables, particularly habitat diversity, the results presented may be useful for restoration projects needing to determine the physical requirements of aquatic invertebrate communities. We can apply this knowledge specifically to other peatland pools both regionally and on a wider geographic scale. Conservationists dealing with discrete patches of other habitat types, which may have become fragmented due to habitat degradation, can treat these patches as habitat 'islands' and apply these results to their own systems. Importantly, results can be applied to the wide field of ecological theory, advancing our understanding of the mechanisms underlying species-area relationships and community structure by helping to untangle the real significance of area from confounding factors.

1.2 THESIS AIMS

In this thesis I look at the effects of habitat-patch (pool) size on the number of taxa found and on community structure and composition. Using a natural pool complex, in which habitat diversity does not appear to differ across more than an order of magnitude in pool size, I test whether an increase in size alone can explain variation in the number of taxa found.

By looking at patterns in community composition and structure I can also investigate whether separate taxa, or groups of taxa, are responding differently to an increase in pool size. Multivariate methods are used to investigate how composition might change across a habitat-patch size gradient. Pool location within the complex and water chemistry measurements are included in the analyses to determine any confounding influence of these variables. I ask whether taxa are added (or lost) at random with an increase in pool size or whether only certain taxa or groups of taxa are affected. I investigate changes in the relative proportions of taxa at different trophic levels within the pools by comparing ratios of the number of predator:prey taxa across the size gradient and also across the gradient of taxon richness. I consider the relationship between species' abundance and occupancy of pools within the complex and whether groups of similar taxa (e.g. by taxonomic groups or body size) display idiosyncratic patterns.

When habitat patches are close together in space, the level of connectedness between them is important in determining whether each assemblage functions independently of the surrounding habitat patches. By determining similarities or differences between the different study-pool assemblages, I can investigate whether each pool functions as a discrete and independent community determined by individual factors, or whether the whole complex is acting as a single community consisting of a series of highly interconnected habitat-patches.

1.3 THESIS STRUCTURE

In Chapter 2 I describe the study site in detail. This is important in this research project in order to identify any factors that may confound pool size. The

physical dimensions of the pools and water chemistry measurements are reported in this chapter.

Chapter 3 presents the results of the survey of the invertebrate populations and briefly discusses the conservation status of some of the species found. I describe the relative abundances of the invertebrate groups that were collected and compare within-group diversity. Three different sampling methods were used and I discuss these in respect to their efficiencies at collecting different types of taxa. For example, sampling the pool sediment was an efficient way of collecting the more sedentary taxa of the benthos, whilst activity traps were more efficient at collecting the mobile taxa of the water column. I also discuss the seasonal changes observed in species composition, which may have an important effect upon the internal dynamics of the community.

In Chapter 4 I test whether there is a relationship between the number of taxa found in standardised sampling units and pool size. Simple linear regression analysis was carried out on each of the three sampling methods to test for an effect of pool area. Patterns at the whole assemblage level may mask or reflect patterns at lower levels within the community, therefore taxon richness within separate taxonomic (e.g. Coleoptera) and functional (e.g. predatory) groups were calculated and regressed against pool area.

In Chapter 5, multivariate methods were used to investigate differences in community composition along the pool size gradient. Pool location within the complex and water chemistry results were also included in these analyses. Abundance-occupancy relationships were plotted for each of the three sampling methods to examine distribution patterns across the complex. To examine trophic

structure over the size gradient, predator:prey ratios were calculated and the proportion of predators was regressed against pool area. The proportion of predators was also regressed against taxon richness.

In Chapter 6 I discuss the overall significance of my results and how they can be interpreted to advance our understanding of the effect of habitat-patch size on the faunal assemblages within them. The respective differences in the way individual taxa, or groups of taxa, respond to a pool size gradient are considered and the underlying mechanisms responsible for creating patterns in distribution across the pool complex are discussed. The extent and nature of connectedness between the pools is discussed with respect to whether the pool complex functions as a series of individual ecological 'islands' or as a single, inter-connected community.

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2 Site Description

2.1 THE FLOW COUNTRY OF CAITHNESS AND SUTHERLAND

The Flow Country of Caithness and Sutherland, in northern Scotland, is a complex peatland ecosystem with a surface dominated by *Sphagnum* and other mosses, interspersed with heather (e.g. *Calluna vulgaris* (L.) Hull), bog myrtle (*Myrica gale* L.) and other vascular plants. The total extent of the peatland has been estimated at 401,375 hectares (Lindsay *et al.*, 1988) making it the largest blanket mire in Europe. Mires require a particular combination of environmental conditions to develop; a cool, continuously wet climate with a waterlogged and deoxygenated ground surface. These specialised, somewhat hostile, environments often contain rare species and unique combinations of both fauna and flora. For example, the blanket bog of the Flow Country is an important breeding area for bird populations including greenshank (*Truing nebularia*), golden plover (*Pluvialis apricaria*), dunlin (*Calidris alpina*) and arctic skua (*Stercorarius parasiticus*). Raptors such as hen harriers (*Circus cyaneus*), golden eagles (*Aquila chrysaetos*) and merlins (*Falco columbarius*) also breed and feed in this habitat. The unique combination of avifauna it supports is not found anywhere else in the world (Lindsay *et al.*, 1988). European mires host many species of plants and animals that are rarely found in other habitats (or at least have the majority of their distribution on mires). These include aquatic *Sphagnum* mosses, shrubs such as *Myrica gale* L., butterworts (*Pinguicula* spp.), carnivorous plants such as the sundews (*Drosera* spp.), biting midges (*Culicoides* spp.) and several species of aquatic beetle (Friday, 1988).

Groups of small pools sporadically pattern the large expanses of blanket bog, often accompanied by larger lochs (Glaser, 1998; Belyea & Lancaster, 2002). These pools are generally acidic, fishless and support many species of invertebrates and plants, some of which are peculiar to this type of habitat (e.g. the Northern Damselfly, *Coenagrion hastulatum* (Charpentier), and the bog-bean, *Menyanthes trifoliata* L. Invertebrate communities often reflect the near tundra-like characteristics of the area with many northern and boreal species representing the southernmost point of their distributions (Lindsay, 1995).

2.2 FORSINARD

The study site is a bog pool complex approximately 155 m a.s.l. at Forsinard (58°22′6′′ N, 3°54′54′′ W) within the Flow Country of north-eastern Scotland (Figure 2.1). The pools are located on a Royal Society for the Protection of Birds reserve, which is also a designated Site of Special Scientific Interest. The surrounding area is blanket bog managed for grouse, red deer and as an RSPB reserve. Local afforestation and peat cutting, which often affects the drainage of nearby pools, has not occurred in the area immediately surrounding the complex and the pools appear to be more or less undisturbed by humans. Mean annual temperatures range from 7.5-8.0 °C, with total annual precipitation 650-1000 mm over 180-200 days (Lindsay *et al.*, 1988). The underlying geology is granite and allied rocks together with granulites and schists (Johnstone & Mykura, 1989).

The complex consists of 641 permanent pools confined within an area of less than 0.25 km^2 and is typical of the many pool complexes found within the Flow Country. The complex is located on the top of a broad ridge that slopes gradually

downward north north east and more steeply east south east and west north west. The pools form discrete bodies of water contained within the peat, which is approximately 3 m deep (Belyea & Lancaster, 2002). The pools do not extend down as far as the underlying mineral substrate. The surrounding blanket bog is covered with mosses such as *Sphagnum* spp. and *Racomitrium lanuginosum* (Hedw.) Brid., sedges such as *Trichophorum caespitosum* (L.) Hartman, *Eriophorum* spp. and *Carex* spp. and small shrubs such as *Calluna vulgaris* and *Myrica gale*. The pool bottom surfaces are limnic sediments with some covering of benthic algae which include diatoms, desmids and some cyanobacteria. The shallow margins of some pools contain aquatic and semi-aquatic *Sphagnum* mosses and *Eriophorum*. In most pools, emergent stands of *Menyanthes trifoliata* are present in varying densities.

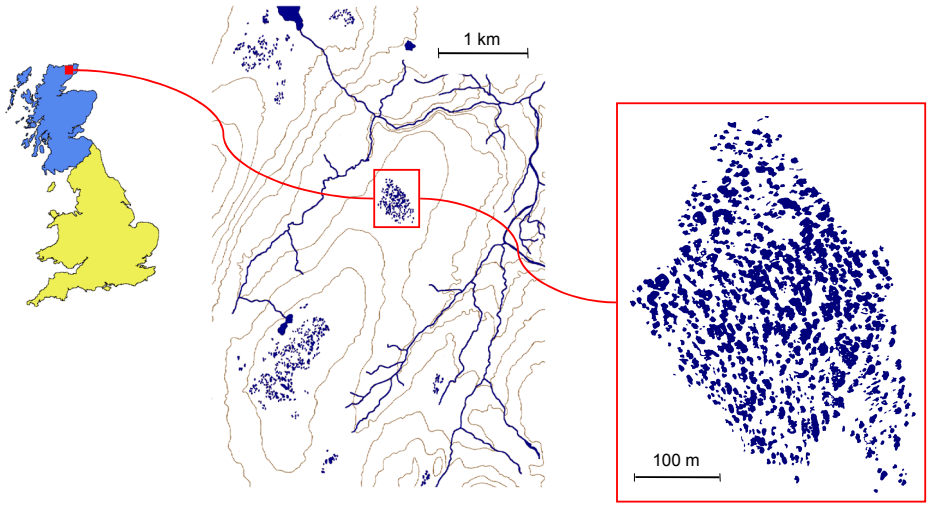

Figure 2.1. The bog-pool complex at Forsinard in Northern Scotland

Twenty-two permanent pools, roughly elliptical in shape, were surveyed (Figure 2.2). Criteria used to select pools was that they must be permanent and that they were regular in shape (some pools had highly convoluted perimeters, thus

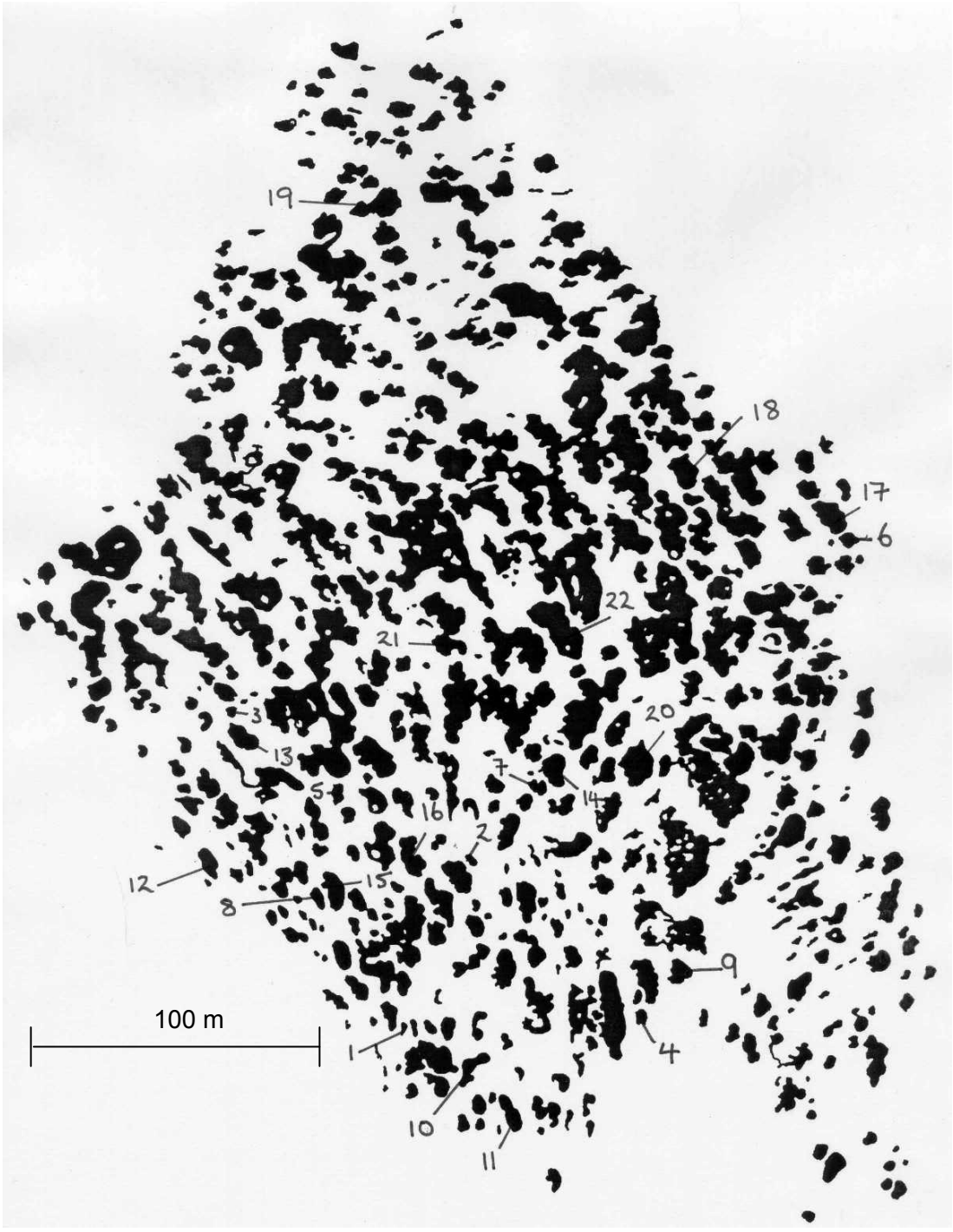

Figure 2.2. Map showing the position within the complex of each of the study pools. Pools are numbered 1 – 22 in increasing size order.

changing perimeter:area ratios in comparison to the more regularly shaped pools). Permanence was defined as those pools having a peaty brown bottom without encroaching terrestrial grasses or *Sphagnum*, indicating they do not dry out even during periods of drought. Permanence was verified by confirming these pools were clearly visible in aerial photographs taken in both 1946 and 1989.

2.2.1 Physical and chemical properties of the Forsinard pools

Pool surface area measurements for all 641 pools range from 2.3 m^2 to 1930 m^2 (Belyea & Lancaster, 2002). The 22 pools used in this study were roughly elliptical in shape ranging in area from 8.6 m^2 to 280.9 m^2 (Figure 2.3), over an order of magnitude in difference. Pools outwith this range were either too small to be considered permanent or so large they appeared to be a series of connected smaller pools and were highly irregular in shape.

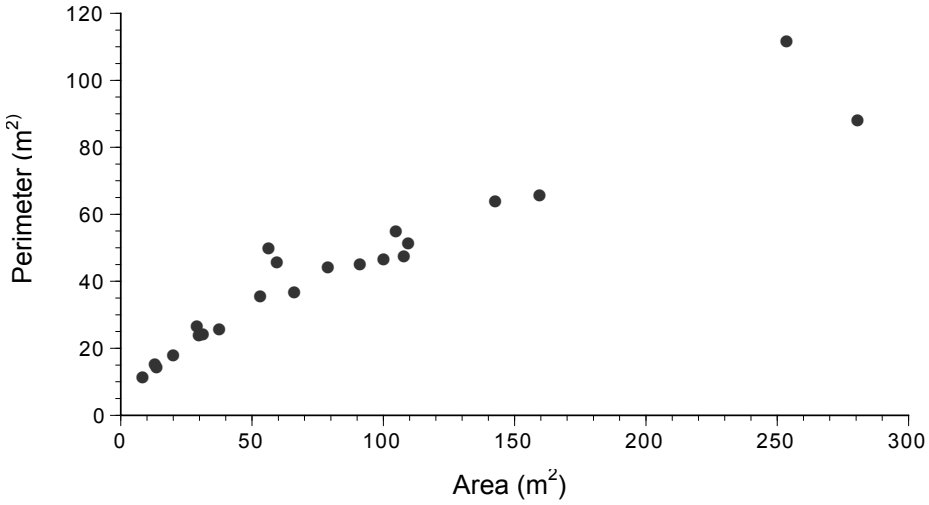

Figure 2.3. Pool perimeter plotted against pool area to demonstrate the extent of the pool size gradient used in this study.

Table 2.1. Physical dimensions of the 22 study pools showing area, maximum length (Lmax), maximum width perpendicular to Lmax (Wmax), Perimeter (Perim.), and maximum depth (Dmax), and median depth (Dmed) measured along length and width transects.

Pool No.	Area (m^2)	Lmax (m)	Wmax (m)	Perim. (m)	Dmax (m)	Dmed (m)
1	8.59	5.0	2.5	11.19	0.22	0.13
2	13.28	6.0	4.0	14.87	0.36	0.29
3	14.06	5.0	4.0	13.99	0.31	0.14
4	20.31	7.0	5.0	17.74	0.46	0.24
5	29.30	10.0	5.0	26.43	0.38	0.20
6	30.08	9.0	6.0	23.71	0.50	0.24
7	31.64	8.5	6.0	24.08	0.48	0.26
8	37.89	10.0	5.0	25.33	0.44	0.25
9	53.52	11.0	9.0	35.27	0.60	0.29
10	56.64	16.5	6.0	49.62	0.40	0.28
11	59.77	16.0	5.0	45.51	0.44	0.27
12	66.41	14.5	7.0	36.52	0.50	0.32
13	79.30	14.5	7.0	43.95	0.80	0.34
14	91.41	15.0	11.0	44.84	0.86	0.37
15	100.39	16.0	9.0	46.30	0.78	0.36
16	105.08	17.0	9.0	54.62	0.88	0.39
17	108.20	15.0	10.0	47.12	0.60	0.36
18	109.77	15.0	11.0	51.24	0.62	0.38
19	142.97	20.0	11.0	63.61	1.00	0.41
20	159.77	19.0	12.0	65.38	0.80	0.35
21	253.91	27.5	14.0	111.47	0.85	0.39
22	280.86	27.0	13.0	87.76	0.88	0.48

Each pool used in the study was steep sided and shallow with a flat, peaty bottom surface and a deeper trench along one long side which appears to be caused by hydrostatic pressure exerted on the down-slope ridge (Belyea & Lancaster, 2002). Pool water depth was measured along the maximum length and perpendicular maximum width at 1 m intervals or 0.5 m intervals for pools less than 15 m^2. A perforated, weighted plastic square (15 cm x 15cm) was lowered until it rested on the bottom sediment and water depth was measured to the nearest 2 cm. Depths of the pools varied by only a small amount both within and between pools (Table 2.1). The pools used in the study were all <50 cm deep along the flat pool bottom and ≤1 m

deep along the trench. Individual microhabitats were consistent between pools, each having a vegetated perimeter, steep walls and a brown peaty bottom.

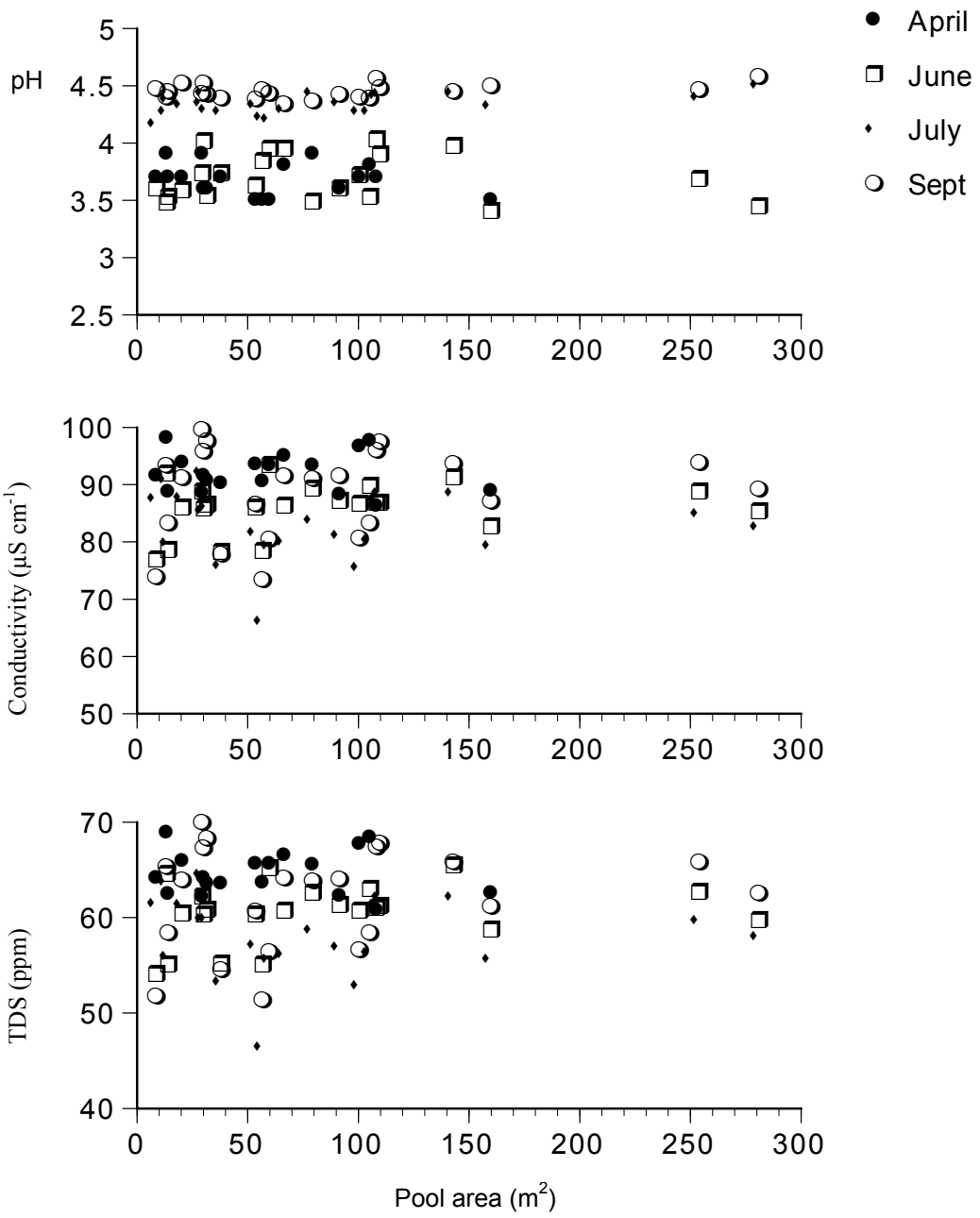

Figure 2.4. Water chemistry recorded for each pool on four sampling occasions during 1999. (Some data are missing due to equipment failure.)

Water conductivity, pH and total dissolved solids (TDS) were measured directly from the pools, using a Whatman® PHA 325C pH/conductivity meter, on four occasions during 1999 (Figure 2.4). Conductivity and TDS showed some differences between seasons but regression analysis revealed no relationship with pool area (Table 2.2). There was some variation in pH between months and a weak positive correlation with pool area in July 1999 (Table 2.2). No other occasion showed a relationship between pool area and pH. Based on this information, the pools used in this study can be considered to be similar in all aspects except size.

Table 2.2. Regression results of pH, conductivity and total dissolved solids (TDS) on pool area for four sampling occasions during 1999 showing R^2 and P. The only significant result ($P < 0.05$) is shown in bold.

	pH		Conductivity (μS cm^{-1})		TDS (ppm)	
	R^2(%)	P	R^2(%)	P	R^2(%)	P
April	0.0	0.367	0.0	0.734	0.0	0.753
June	0.0	0.665	0.0	0.327	1.8	0.254
July	**24.1**	**0.012**	0.0	0.838	0.0	0.873
Sept	10.2	0.081	0.0	0.451	0.0	0.444

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3 Peatland pool invertebrate assemblages

3.1 INTRODUCTION

The invertebrate fauna of the peatland bog pools at Forsinard are currently poorly described. This chapter provides a detailed survey of the fauna, from the microcrustacea to large predators. The pool complex at Forsinard is typical of the many bog pool complexes found in the Flow Country and this survey is not only a valuable study of aquatic invertebrates found in the area, but also provides a useful reference to future studies of other, similar, sites.

Peatland ecosystems in Britain have been described in great detail. Many publications discuss their physical characteristics and formation (Clymo, 1987; Lindsay, 1995; Charman, 1998; Belyea & Lancaster, 2002) and their flora (Ratcliffe, 1964; Rodwell, 1991). The avifauna also attracts much attention, largely due to the work of the Royal Society for the Protection of Birds. Invertebrate faunas, particularly aquatic invertebrates, have received less attention. Within the Flow Country in northern Scotland, only the aquatic Coleoptera have been the subject of detailed surveys (Foster, 1988) although other studies surveyed more taxonomic groups of aquatic macroinvertebrates at specific locations (Downie *et al.*, 1998a; 1998b; Standen, Rees & Foster, 1998). Taxa such as the Diptera and microcrustacea have been overlooked, largely due to difficulties with identification. Crisp & Heal (1998) surveyed microfauna in a range of mires in Western Ireland, the English Lake District, the Pennines and Northumberland but none in the Flow Country.

The Scottish flows are a unique habitat and are of international significance for conservation (Lindsay, 1995), supporting many species of both plants and animals that are found in only wet, temperate conditions. Many of the aquatic insects found in the Flows are of intrinsic conservation value and may contribute to the overall functioning of the ecosystem. Aquatic invertebrates are an important food source for wading birds in peatland ecosystems (Stroud *et al.*, 1987; Avery, 1989; Downie *et al.*, 1998b) and for palmate newts and frogs which are also found on these mires. Many peatland species are poorly described and studies of aquatic invertebrates in the Scottish Flows can help us to understand their distribution, abundance and importance to the surrounding ecosystem.

In previous studies, sampling has often involved sweeps with a pond net along the pool margin, which can be destructive in fragile habitats. In these pools, the soft, flocculent nature of the bottom sediments means they can easily be disturbed obscuring any view of the water column and also clogging the net. Therefore, sweep netting is an impractical, as well as destructive, method for sampling peatland-pool benthic fauna. Looking at macroinvertebrates in bog pools, Downie *et al.* (1998a) collected samples with activity traps. These allow swimming fauna to enter the trap without disturbing sediment or damaging vegetation and are thus less destructive than sweep-netting methods.

This chapter expands our knowledge of peatland pool invertebrates by providing a comprehensive survey of the invertebrate fauna, from microcrustacea to large predators, in a typical bog pool complex representative of the Flow Country of northern Scotland. Relative abundances of the invertebrate fauna were compared together with species diversity amongst taxonomic groups. In order to sample both

the water column and the benthos, baited and unbaited activity traps together with a quantitative bottom sampler were used to establish which method, or combination of methods, is most efficient to survey this type of habitat. Seasonal variation in the relative abundance of different taxonomic groups is also investigated.

3.2 METHODS

3.2.1 Invertebrate sampling and identification

In order to sample the entire community, and for animals that differ in mobility, I used two sampling methods suitable for the different microhabitats within the pools. Activity traps were used to catch animals swimming in the water column and crawling or swimming along the pool bottom. Benthic sediment samples collected animals living in the soft sediments and with a more sedentary life style. Bog pools take hundreds or thousands of years to form and, being extremely fragile, can take years to recover from physical damage due to the slow processes involved in their formation (Belyea & Lancaster, 2002). Care was therefore taken to minimise disturbance and all sampling was undertaken from the bank. It was impossible to wade into the pools, as the bottom was too soft.

Activity traps were based on designs previously found to be effective at catching mobile invertebrates (Aiken & Roughley, 1985; Lancaster & Scudder, 1986; Ulrich, 1986; Downie *et al.*, 1998a). Each trap consisted of a length of opaque PVC pipe 250 mm long, 100 mm internal diameter. Mesh (250 μm) was placed over one end of the pipe and an inverted funnel (internal diameter 20 mm at the narrowest end) placed in the other end. This allows animals to enter the trap through the funnel but provides only a narrow aperture from which they can escape. Animals therefore

remain trapped in the pipe. Some traps were placed horizontally in the water column (WCs) approximately 0.5 m from the bank and 0.2 m below the surface, suspended from bamboo canes by fishing line. These traps contained a Cyalume® lightstick inside to attract animals at night. Other traps were placed on the pool bottom (Sinkers) parallel to, and approximately 0.5 m from, the bank. These traps contained no light as preliminary tests had shown traps placed on the bottom caught slightly more animals than those in the water column. All traps were left in the pools for seventy-two hours.

Predatory diving beetles may be important members of pool communities because of their trophic status, abundance, and mobility. However being highly mobile they can often be difficult to trap. To enhance capture of these beetles, one WC and one Sinker trap were baited with a small piece of meat (cat food), placed in each pool and left for twenty-four hours.

Sediment samples were collected with a quantitative bottom sampler which consisted of a rectangular plastic frame (25 cm x 15 cm) attached to a pole to facilitate sample collection from the bank. A nylon skirt was attached to the bottom of the frame that could be opened and folded back over the sides. The frame was pushed approximately 2 cm into the sediments with the skirt folded back. A drawstring running through the edge of the skirt was then pulled tight and up through the inside of the frame, thereby creating a tight seal and isolating the soft surface sediments. Samples were collected approximately 0.5 m from the pool edge, the limit of an arm's reach.

Twenty-two pools were sampled along a size gradient. In an effort to scale sampling effort towards pool surface area, more samples were taken from the larger

pools (Table 3.1). The scaled sampling was not intended to be proportional, but to increase the number of samples taken in the larger pools.

Table 3.1. Pool surface area showing numbers of baited and unbaited traps per pool in the water column (WC) or on the bottom (Sinker) and number of sediment samples. Size category (Size cat.) is shown which is an arbitrary division made to allocate different numbers of activity traps and benthic samples along the pool size gradient. Total numbers of each trap type per pool are shown in bold.

Pool No.	Size (m^2)	Size Cat.	Baited		**Total Bait**	Unbaited		**Total Unbaited**	**Total Sediment**
			WC	Sinker		WC	Sinker		
1	8.5	S	1	1	**2**	1	1	**2**	**1**
2	13.2	S	1	1	**2**	1	1	**2**	**1**
3	14.0	S	1	1	**2**	1	1	**2**	**1**
4	20.3	S	1	1	**2**	1	1	**2**	**1**
5	29.3	M	1	1	**2**	2	1	**3**	**2**
6	30.0	M	1	1	**2**	2	1	**3**	**2**
7	31.6	M	1	1	**2**	2	1	**3**	**2**
8	37.8	M	1	1	**2**	2	1	**3**	**2**
9	53.5	M	1	1	**2**	2	1	**3**	**2**
10	56.6	M	1	1	**2**	2	1	**3**	**2**
11	59.7	M	1	1	**2**	2	1	**3**	**2**
12	66.4	M	1	1	**2**	2	1	**3**	**2**
13	79.3	M	1	1	**2**	2	1	**3**	**2**
14	91.4	M	1	1	**2**	2	1	**3**	**2**
15	100.3	L	1	1	**2**	3	2	**5**	**3**
16	105.0	L	1	1	**2**	3	2	**5**	**3**
17	108.2	L	1	1	**2**	3	2	**5**	**3**
18	109.7	L	1	1	**2**	3	2	**5**	**3**
19	142.9	L	1	1	**2**	3	2	**5**	**3**
20	159.7	L	1	1	**2**	3	2	**5**	**3**
21	253.9	L	1	1	**2**	3	2	**5**	**3**
22	280.8	L	1	1	**2**	3	2	**5**	**3**

Scaling may provide a more thorough spatial sampling of larger habitats (by using different combinations of random samples from the larger systems) and allow a test (albeit imperfect) to be made of something closer to the true species-area effect (i.e. this method is closer to that which a complete census might achieve) than if no scaled sampling were available. The multiple-sample system can also be used to test for evidence of sample completeness, i.e. how effectively a single sampling-unit collects species. An important practical consideration in scaling the sampling was to avoid over-sampling, and therefore damaging, the smallest pools.

The pool size-groups were decided during an early visit to the site by how many samples it was felt could be used without over-sampling the pool. Sampling was repeated four times at six-weekly intervals between April and September 1999.

All specimens collected were preserved in 70% IMS and identified to the lowest taxonomic level possible. Hydracarina (water mites) were identified to order and Oligochaetae were identified to class. Chironomidae found in sediment samples were identified to genus. Where several visually distinct species within a single genus of chironomid were observed, they were identified as Species A, Species B, etc. Chironomids were uncommon in activity traps where they were identified to family only. All other individuals were identified to species or to the lowest taxonomic level possible. Taxonomic resolution amongst pools remained consistent, ensuring equal bias across all pools. Using reference to the literature, the fauna were classified as predators, herbivores or 'other'. Predators were defined as those which are strict carnivores, herbivores as those which eat only live plant matter and 'other' as any taxa which does not fit into either the predator or herbivore category. This latter category includes taxa that are detritivores, taxa that are mainly detritivores but may occasionally scavenge some food items (e.g. the Corixidae) and taxa that may show an ontogenetic shift in diet and eat both animal and non animal food items during their aquatic life cycle (e.g. the Phryganeidae, (Solem & Gullefors, 1997)).

Sediment samples were sieved through a 250 μm sieve. The animals were then sorted without magnification. Due to their small size, Hydracarina, Oligochaetae and the microcrustacea were not collected from these samples. Activity traps contained little sediment and did not require sieving. Due to the small size of many of the animals collected using this method they were sorted under a

microscope. Macroinvertebrates were identified using a Leica MZ6 dissecting microscope (up to 40× magnification). Microcrustacea (Cladocera and Copepoda) were identified using both a Leica MZ6 dissecting microscope (100× magnification) with a sub-stage light source and by slide-mounting samples and using an Olympus BX40 compound microscope when necessary. Chironomids were identified to genus by slide mounting the heads and bodies separately and using an Olympus BX40 compound microscope. All slides were prepared using either glycerol or Aqua-mount.

3.2.2 Statistical analysis

The numbers of individuals in each taxonomic group were not normally distributed and variances among the data were heterogeneous even after logarithmic transformation. Therefore, to test for differences between numbers of individuals among sampling methods, the nonparametric Kruskal-Wallis test was used (Zar, 1999). This test, which looks for differences among the sample medians, was used to test for differences in the number of individuals within a taxon among all three sampling methods (baited activity traps, non-baited activity traps and sediment samples) and then for differences between the baited and the non-baited activity traps. For each sampling method, data for all twenty-two pools and all four sampling occasions were pooled and the median number of taxa, or taxonomic groups, per sample was calculated. Due to the similarity of type of trap, time left in the pool and the similarity in catch, Sinker and WC non-baited activity traps were not differentiated in these analyses.

3.3 RESULTS

Sixty-nine different taxa were collected and identified from 22 pools over the four sampling periods during 1999. Within 13 orders, 48 were identified to species and a further 17 to genus, shown in Table 3.2 below.

Table 3.2. List of taxa, trophic status and frequency of occurrence of invertebrate taxa. P = predator, H = herbivore, O = other (mostly detritivores). Pool frequency (Pool freq.) shows number of pools out of 22 in which a species was found during 1999; + = species found or seen in pools that were not included in this study, or seen in study pools but not collected in study samples; * indicates a completely aquatic lifestyle at all stages of development.

Order	Family (Sub-family)	Species name	Trophic status	Pool freq.
Calanoida*		*Diaptomus gracilis* Sars	H	19
Cyclopoida*		*Acanthocyclops vernalis* (Fischer)	P	22
		Paracyclops sp.	H	22
Harpacticoida		Undetermined	H	2
Cladocera*	Sididae	*Diaphanosoma brachyurum* Liéven	H	4
		Latona setifera (Müller)	H	3
	Daphniidae	*Ceriodaphnia setosa* Matile	H	22
	Bosminidae	*Bosmina coregoni* Baird	H	11
	Macrothricidae	*Acantholeberis curvirostris* (Müller)	H	22
		Drepanothrix dentata (Eurén)	H	22
		Ilyocryptus sordidus (Liénen)	H	21
	Chydoridae	*Acroperus harpae* Baird	H	22
		Alonopsis elongata Sars	H	22
		Alona guttata Sars	H	22
		Alona rustica T. Scott	H	17
		Alona affinis/quadrangularis	H	16
		Alona elegans (Kurz)	H	2
		Alonella excisa Fischer	H	14
		Alonella nana Baird	H	22
		Chydorus sphaericus (Müller)	H	22
		Graptoleberis testudinaris (Fischer)	H	19
	Polyphemidae	*Polyphemus pediculus* (L.)	P	21
Oligochaetae*		Undetermined	O	19
Acarina*	Hydracarina	Undetermined	P	22
Ephemeroptera	Leptophlebidae	*Leptophlebia vespertina* (L.)	O	22
Odonata	Coenagrionidae	*Coenagrion hastulatum* (Charpentier)	P	17
	Aeshnidae	*Aeshna juncea* (Linné)	P	3
	Libellulidae	*Libellula quadrimaculata* (Linné)	P	6
		Sympetrum danae (Sulzer)	P	10
Hemiptera	Corixidae (Corixinae)	*Glaenocorixa propinqua* (Fieber)	O	1
		Callicorixa wollastoni (Douglas & Scott)	O	6
		Hesperocorixa castanea (Thomson)	O	1
		Sigara nigrolineata (Fieber)	O	+
		Sigara scotti (Douglas & Scott)	O	19

Table 3.2 continued.

Order	Family (Sub-family)	Species name	Troph. status	Pool freq.
Megaloptera	Sialidae	*Sialis lutaria* (L.)	P	13
Coleoptera	Gyrinidae	*Gyrinus minutus* Fabricius	P	7
	Dytiscidae			
	(Hydroporinae)	*Hydroporus erythrocephalus* (L.)	P	4
	(Colymbetinae)	*Agabus arcticus* (Paykull)	P	9
		Ilybius aenescens Thomson	P	17
		Ilybius guttiger (Gyllenhal)	P	1
		Rhantus suturellus (Harris)	P	5
		Colymbetes fuscus (L.)	P	2
	(Dytiscinae)	*Acilius sulcatus* (L.)	P	16
		Dytiscus marginalis L.	P	8
		Dytiscus lapponicus Gyllenhal	P	18
		Dytiscus semisulcatus Müller	P	1
Trichoptera	Polycentropodidae	*Cyrnus flavidus* (McLachlan)	P	18
	Limnephilidae	*Lymnephilus stigma* (Curtis)	O	2
		Nemotaulius punctatolineatus (Retzius)	O	+
	Phryganeidae	*Agrypnia obseleta* (Hagen)	O	19
		Phryganea bipunctata (Retzius)	O	10
Diptera	Chaoboridae	*Chaoborus obscuripes* (van der Wulp)	P	22
	Ceratopogonidae	*Culicoides* sp.	O	17
	Chironomidae			
	(Tanypodinae)	*Ablabesmyia* sp.	P	22
		Macropelopia sp.	P	22
		Procladius sp.	P	22
	(Orthocladiinae)	*Acamptocladius* sp.	O	1
		Corynoneura sp.	O	2
		Heterotrissocladius sp.	O	1
		Psectrocladius sp. A	O	21
		Psectrocladius sp. B	O	22
		Psectrocladius sp. C	O	22
	(Chironominae)	*Chironomus* sp./*Einfeldia* species group C	O	22
		Dicrotendipes sp.	O	16
		Microtendipes sp.	O	4
		Pagestiella sp.	O	22
		Polypedilum sp.	O	2
		Sergentia sp.	O	21
		Tanytarsus sp.	O	22

Twenty-four taxa were predators, 20 were herbivores and 23 were allocated to the category ‘other’. Cladocerans (of which 17 taxa out of 18 were herbivores) were the largest taxonomic group with respect to both number of taxa and abundance, accounting for 26% of the total taxa recorded (Figure 3.1) and 58% of the total number of individuals collected (Table 3.3). Diptera (mainly Chironomidae

larvae) were equal in number of taxa (26%) and the next largest group in number of individuals (29%). Coleopterans were the third most diverse group (16%) and the Copepoda the third most abundant group (10%). Two IUCN British Red Data Book species were recorded: the Northern Damselfly, *Coenagrion hastulatum* (Charpentier), and the cased caddisfly, *Nemotaulius punctatolineatus* (Retzius). Three species of aquatic Coleoptera were collected which have Nationally Notable status according to Ball (1986): *Dytiscus lapponicus* Gyllenhal, *Ilybius aenescens* Thomson and *Gyrinus minutus* Fabricius.

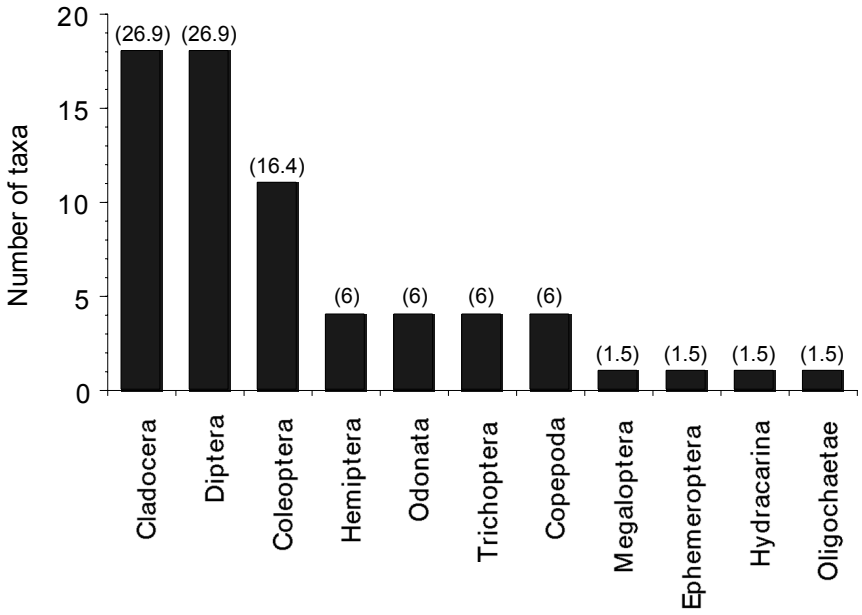

Figure 3.1. Number of taxa in each major taxonomic group found in all 22 pools over 4 sampling periods. Hydracarina and Oligochaetae are identified to order only. Chironomidae (Diptera) are identified to genus only. Number of taxa within each group, as a percentage of total taxa, is given in parenthesis above the relevant bar. See Table 3.3 for number of individuals.

Table 3.3. Number of individuals within each taxon from the total sampling effort.

Taxonomic Group	Individual abundance	% abundance
Cladocera	44,772	58.0
Diptera	22,312	29.0
Coleoptera	395	0.5
Hemiptera	121	0.2
Odonata	56	0.1
Trichoptera	212	0.3
Copepoda	7,441	10.0
Megaloptera	21	<0.1
Ephemeroptera	403	0.5
Hydracarina	674	0.9
Oligochaetae	200	0.3

Table 3.4. Comparison of sampling efficiency (measured by number of individuals per sample) for each sampling method using a Kruskal-Wallis test. Mean abundance is shown rather than the median for comparison only (median values were zero to several decimal places for most groups). The Kruskal-Wallis H statistic is given for comparing differences between the medians of all methods (DF = 2) and, where sediment sampling was not the most efficient method of collecting, baited vs. unbaited activity traps only (DF = 1). Where a result is significant, the highest mean value is shown in bold. * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, NS = not significant.

	Mean no. individuals per sample			Kruskal-Wallis H statistic	
Taxon	Benthic samples	Baited activity traps	Unbaited activity traps	All methods	Baited vs. unbaited activity traps
Newt/tadpole	0	0.048	**0.076**	12.34**	-
Cladocera	-	65.766	**111.148**	-	17.06***
Chironomidae	**105.901**	4.707	5.342	352.6***	-
Chaoboridae	0.558	0.096	**1.786**	44.46***	43.73***
Ceratopogonidae	**0.198**	0.138	0.046	20.91***	-
Coleoptera (ad.)	0.012	**0.731**	0.411	69.53***	9.86**
Coleoptera (l.)	**0.506**	0.102	0.122	46.43***	-
Hemiptera	**0.314**	0.054	0.109	24.21***	-
Odonata	0.087	0.048	0.099	2.53 NS	-
Trichoptera	**0.773**	0.108	0.151	116.58***	-
Copepoda	-	11.156	**18.352**	-	42.19***
Megaloptera	**0.110**	0.000	0.003	40.45***	-
Ephemeroptera	0.052	0.168	**1.039**	79.47***	34.6***
Hydracarina	-	1.545	1.368	-	1.19 NS
Oligochaetae	-	0.467	0.401	-	0.04 NS

3.3.1 Sampling method efficiency

The three sampling methods used to collect invertebrates from the pools differed in sampling efficiency. Benthic samples were more effective than activity traps at collecting Hemiptera, Megaloptera, larval Coleoptera, Trichoptera, Ceratopogonidae and Chironomidae (Table 3.4). For the remaining taxonomic

groups, baited and non-baited activity traps were compared and were shown to differ in the relative abundances of taxa collected. Baited traps were more efficient at catching adult Coleoptera than unbaited traps. Unbaited activity traps caught more Copepoda, Cladocera, Ephemeroptera and Chaoboridae than the baited traps, which was likely due to the increased time period involved.

3.3.2 Seasonal variation

Some effects of season for different taxonomic groups were detected in the number of individuals collected in the samples (Figure 3.2). Newts and tadpoles were collected in low numbers during all sampling periods. Adult Coleoptera showed an initial increase in number in June and afterwards no clear seasonal pattern. The larvae showed no clear seasonal pattern throughout. Hemiptera numbers were approximately four times higher in July than in any other month. Approximately double the number of odonates were found in July and September than were found in April and June. Hemiptera appeared to peak in July by almost three times the numbers found in other months. Trichoptera numbers increased over the four sampling periods whilst Ephemeroptera showed almost the opposite effect and decreased to almost absent in July before increasing again. Chaoboridae numbers dipped to almost zero in June and peaked in September to almost four times the numbers found in July. Hydracarina were at their highest, by over two times, in April then decreased steadily after an initial steep drop. Chironomid larvae displayed a decrease from April to September to less than half the original numbers present. Cladocera reached a peak in July before dropping in September and the Copepoda were at their highest in June.

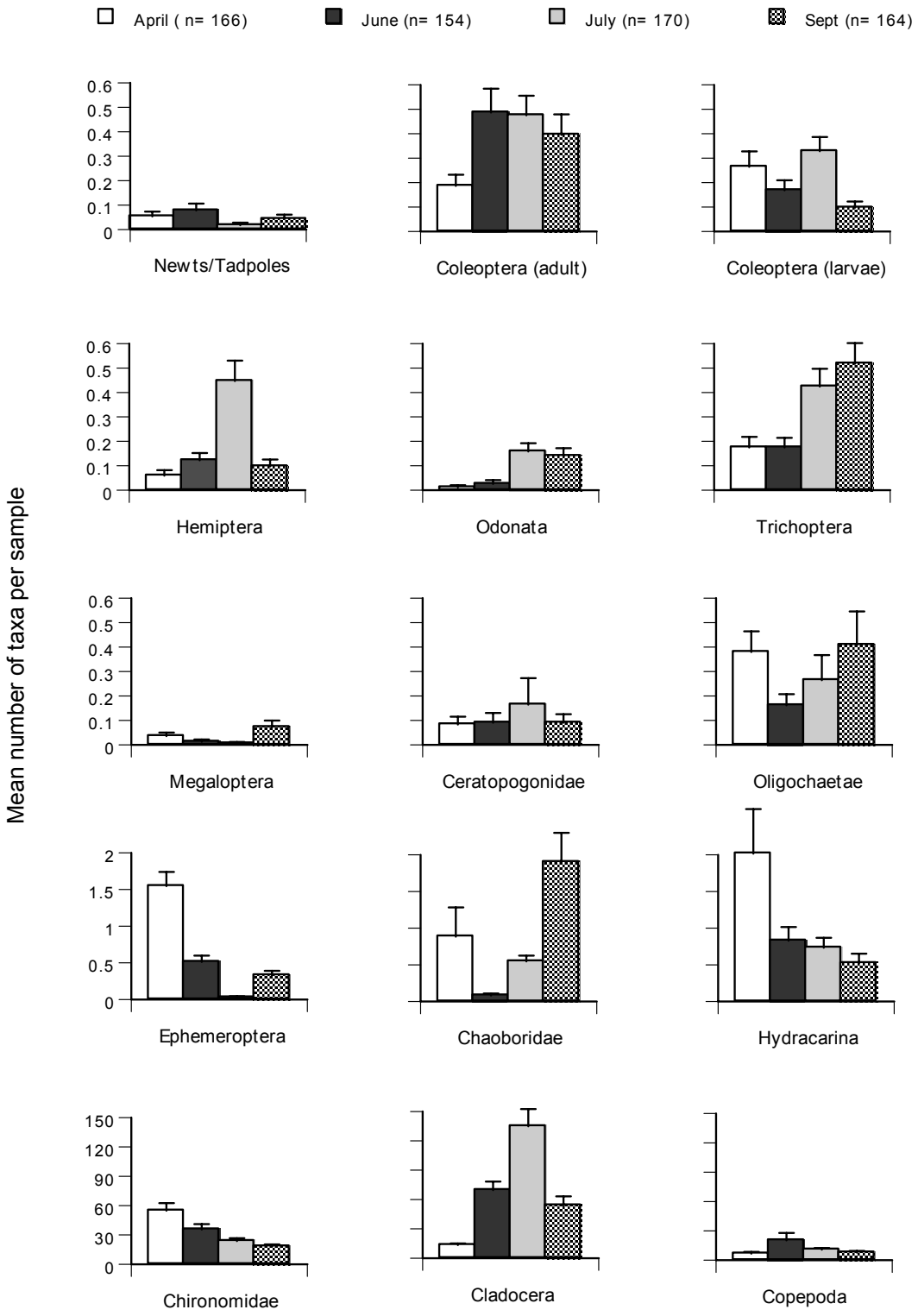

Figure 3.2. Seasonal variation of mean number ± SE of individuals found per sample over four sampling periods. All sampling methods have been combined except for Oligochaetae, Hydracarina, Cladocera and Copepoda where only activity traps were included as benthic samples were not used to collect these taxa.

3.4 DISCUSSION

3.4.1 Species assemblages

The peatland pools at Forsinard hosted a fauna typical of this type of habitat. Coleoptera were the dominant predators in these dystrophic pools. All coleopteran species collected were predatory and typical of the Flow Country (Foster, 1988). All four species of Odonata found at this site have been recorded as breeding in acid bog pools (Hammond, 1983; Foster, 1995; Gibbons, 1998; Standen *et al.*, 1998). Ephemeroptera larvae are known to be sensitive to low pH (Elliot, Humpesch & Macan, 1988) and I collected only one species, *Leptophlebia vespertina*, from the pools. This has previously been reported as the only mayfly species present in conditions of low pH (see Elliot *et al.* 1988). It was also the only mayfly species found by Standen *et al*. (1998) in acid mire pools in the Sutherland flows. This obviously acid-tolerant species is likely to be typical of, and the only Ephemeroptera present in, many acid pool sites in northern Scotland.

I have found no detailed records of microcrustacean species in the Scottish flows. In their study of mire pools in Ireland, northern England and Wales, Crisp and Heal (1998), although not publishing any species lists, reported a dominance of *Chydorus sphaericus* from their sites in the Pennines. This is a widespread species (Scourfield & Harding, 1994) and was present in all 22 pools included in this study. All microcrustacean species I collected are widespread and/or typical of acid pools (Scourfield & Harding, 1994). Microcrustacea were found in abundance in both the activity traps placed in the water column and in those placed on the pool bottom. Some of the species collected are known to be benthic (pers. com.) and this is evidence that migration, possibly diurnal, occurs into the water column, probably for

feeding purposes or as a predator-avoidance strategy. The abundance and diversity of these taxa in the pools showed they are an important group in the aquatic fauna and should not be overlooked.

Several of the species collected from the Forsinard pools are officially listed as threatened. *Coenagrion hastulatum*, the northern damselfly, is listed as Category 2 "Vulnerable" in the IUCN British Red Data Book 2: Insects (Shirt, 1987). *C. hastulatum*, which for Britain has only previously been recorded in Inverness-shire, Aberdeenshire and Perthshire (Hammond, 1983), has not officially been recorded in Sutherland. Although rare in Britain, it is the most common and widespread species of the genus in North Europe (Nilsson, 1996). Of the four Odonate species found during this study, *C. hastulatum* was the most widespread and abundant and there was no indication that this population was under threat at this site. Although Hammond (1983) suggests this species is restricted to breeding in marshy margins of sheltered lakes and bog pools, it is likely that its distribution, in Britain at least, is actually more restricted to sheltered margins of bog or acid pools. This would account for its limited geographical distribution. Although it is not uncommon at its known sites and the population in Britain appears to be stable, the localised distribution of *C. hastulatum* means that it is considered highly vulnerable to adverse environmental changes (Hammond, 1983). Poor documentation may be a possible factor in the limited records of this species as bog pools are widely distributed in the north of Scotland.

Another IUCN British Red Data Book species is the cased caddisfly, *Nemotaulius punctatolineatus*. This species has Category 3 status "Rare" (Shirt, 1987) and was found within the pool complex being studied but was not collected in

samples included in the study. Easily spotted by a distinctive case which is sandwiched by two bog bean (*Menyanthes trifoliata* L.) leaves, it was even seen in winter crawling on the underside of the thick ice sheet on one of the pools (pers. obs.). This is the first record for Sutherland and it has only recently been recorded in Britain: the larvae from pools on blanket bog in Caithness and adult records from Aviemore in Speyside, Inverness-shire (Wallace, Wallace & Philipson, 1990). Its Category 3 status is as yet uncertain (Hammond, 1983) and, again, poor documentation may be a possible factor in the limited records of this species.

A number of Coleopteran species collected in this study have Nationally Notable status according to Ball (1986). *Dytiscus lapponicus* is widespread amongst the study pools but has the status Nationally Notable List A. *Ilybius aenescens,* the most abundant and widespread beetle in the complex, has Nationally Notable List B status, as does the whirligig beetle, *Gyrinus minutus.* Again, these species are typical of peatland pools and their limited distribution across Britain is almost certainly due to the limited availability of suitable habitat.

3.4.2 Sampling methods

Approximately one third of the taxa collected were predators. This differs from Gibbons (1998), who found predominantly predators in his pools. Using a zooplankton net, (mesh size unspecified) Gibbons (1998) used sweep-net sampling methods to investigate invertebrate communities in bog pools in Britain. He found mainly predatory species and surprisingly few herbivores or detritivores; his species list included dragonfly and damselfly larvae *(Aeshna* spp., *Sympetrum danae* and *Pyrrhosoma nymphula*), backswimmers *(Notonecta glauca*), waterboatmen *(Corixa*

wollastoni), phantom midge larvae (*Chaoborus*), alderfly larvae (*Sialis lutaria*) adult diving beetles (*Dytiscus* sp. and *Acilius sulcatus*) and a few chironomids (*Chironomus*). No samples were taken from the benthos so the animals collected were biased towards the larger, more mobile species, which are likely to be predators.

Sweep netting, using a 1-mm mesh net, was the only sampling method used in another study by Standen *et al.* (1998) which investigated the distribution and relative abundance of macro-invertebrates in Scottish bog pools with respect to pool type and afforestation at an early stage in the forestry cycle. The most abundant species, over all the pools sampled, were *Leptophlebia vespertina* (a mayfly), *Chaoborus crystallinus* (a phantom midge) and *Hydroporus obscurus* (a beetle), which are all species commonly utilising the water column, together with chironomids (non-biting midges) which are usually abundant in the benthos. These taxa (at genus level) are a subset of the taxa found in this study which may be attributed to the increased range in sampling methods in my study. Other studies using sweep methods (Foster, 1995; Standen, 1999) collected only animals of the pool margins (e.g. Coleoptera, Hemiptera and Odonata) although this may be all that is of interest to the researcher.

Looking at macroinvertebrates in bog pools, Downie *et al.* (1998a) used activity traps to collect samples, which are less destructive than sweep-netting methods. They described the abundant diving beetles (Dytiscidae), waterboatmen (Corixidae) and backswimmers *(Notonecta obliqua*) in detail and largely ignored other taxa. Although activity traps are usually used to catch beetles and other large, mobile species (Aiken & Roughley, 1985; Lancaster & Scudder, 1986; Ulrich, 1986)

they are also very good at catching microcrustacea and other water column species, as these results show (Table 3.4).

It is clear that some taxa are more efficiently collected by benthic sampling and some by activity traps (see Table 3.4) which indicates the importance of sampling both the benthos and the water column in these types of habitat. The different types of activity trap (baited and unbaited) collected different numbers of each taxon and this may be for different reasons. For example, unbaited activity traps collected significantly more Cladocera and Copepoda individuals than the baited traps. This is likely due to the difference in time the traps were left in the pools (72 and 24 hours respectively). However, when the baited catch is multiplied by three to give similar 'trap hours' to the unbaited traps (Table 3.5), 'Bait x 3' is considerably higher than 'No bait', i.e. more than 1/3 of the catch is caught during the first 24 hours. This may be due to a proportion of individuals escaping from the traps, so that the high numbers caught by day 3 is balanced by those escaping. Adult Coleoptera were collected in higher numbers in 24 hours in baited traps than in 72 hours in unbaited traps. They are effective swimmers and their predatory nature would suggest it is the attraction of the bait that causes high numbers of these taxa to be caught in the 24-hour traps. 'Bait x 3' numbers were higher than 'No bait' for several other taxa and this may be due to escapees over three days balancing new arrivals, attraction to the bait or even predation in the unbaited traps over the three day time period (Table 3.5). Unbaited traps collected more individuals of some taxa than 'Bait x 3' (Ephemeroptera, Chaoboridae, Megaloptera) suggesting either slow colonisation rates, repulsion to the bait or predation in the baited traps (possibly due

to the high numbers of Coleoptera). Further experimentation would be required to separate these factors.

Table 3.5. Mean number of individuals per baited traps multiplied by 3 compared with mean number of individuals in unbaited traps. Because unbaited traps were left in the water for approximately 3 times as long as baited traps (see text), this comparison more accurately reflects the 'trap hours'. Explanations given are possible reasons for differences between 'Bait x 3' and 'Unbaited' numbers other than due to chance events. All values that are lower in 'Unbaited' may also be due to escapees. The highest values are shown in bold. Newts/tadpoles are shown for reference only.

Taxon	Bait	Bait x 3	Unbaited	Possible Explanation
Newt/tadpole	0.048	**0.144**	0.076	Attracted to bait
Cladocera	65.766	**197.299**	111.148	Predation in unbaited traps Highly mobile/fast colonisers
Chironomidae	4.707	**14.120**	5.342	Attracted to bait Predation in unbaited traps
Chaoboridae	0.096	0.287	**1.786**	Predation in baited traps Slow colonisers
Ceratopogonidae	0.138	**0.413**	0.046	Attracted to bait
Coleoptera (ad.)	0.731	**2.192**	0.411	Attracted to bait
Coleoptera (l.)	0.102	**0.305**	0.122	Attracted to bait
Hemiptera	0.054	**0.162**	0.109	Attracted to bait Highly mobile/fast colonisers
Odonata	0.048	**0.144**	0.099	Attracted to bait
Trichoptera	0.108	**0.323**	0.151	Attracted to bait
Copepoda	11.156	**33.467**	18.352	Predation in unbaited traps Highly mobile/fast colonisers
Megaloptera	0	0	**0.003**	Slow colonisers
Ephemeroptera	0.168	0.503	**1.039**	Predation in baited traps
Hydracarina	1.545	**4.635**	1.368	Attraction to bait
Oligochaetae	0.467	**1.401**	0.401	Attraction to bait Predation in unbaited traps

These results show that using a combination of sampling techniques is an ideal way of sampling these pools. Collecting a shallow layer of sediment allows sedentary, benthic fauna to be collected and activity traps enable the more mobile taxa of the water column to be caught. All methods display some bias towards certain taxa and this should be taken into consideration when deciding which sampling methods to employ.

3.4.3 Seasonal variations

The invertebrate assemblage of this pool complex changes seasonally and many taxa show patterns consistent with a spring or summer emergence as adults. An increase in numbers of adult Coleoptera collected may indicate emergence has taken place, which coincides with a small drop in the numbers of larvae. The indefinite pattern in numbers of beetle larvae may reflect a two-year larval stage in some species and size frequency would have to be recorded to detect any seasonal pattern. The mayfly, *L. vespertina,* nymphs are considerably more abundant in April and are probably an important prey species at this time. Their reduction in numbers by July reflects the flight period when they emerge as adults (Elliot *et al.*, 1988) and the slight increase in September the subsequent hatching of the next cohort. The Chaoboridae (phantom midges), *C. obscuripes*, show a pattern indicating that the adults have emerged by June and the next cohort has become established by September. The decrease in chironomid numbers from April to September may indicate a staggered pattern of emergence over the summer amongst the different taxa. The cladoceran (mostly herbivores) peak in abundance in July coincides with increased sunlight and possibly a small phytoplankton bloom. These results emphasise the importance of multiple sampling periods throughout the year in order to observe fully the assemblage present. Sampling at only one time of the year may result in species being under- or overestimated or even missed altogether.

3.4.4 Conclusions

In these systems it is appropriate to use a combination of sampling methods including activity traps and benthic samples if the whole invertebrate community is

to be studied. This enables a wider variety of faunal groups to be collected, including the mobile taxa found in the water column and the more sedentary benthic taxa.

The species composition of the study pools sampled is typical of, and unique to, peatland pool habitats. Several of the species found are limited in their distribution across Britain and have been allocated IUCN Red Data Book or Nationally Notable status. There are, therefore, important conservation issues concerning the fauna of peatland pools. The distribution of blanket bog across Britain in which these acidic, nutrient-poor pools occur is restricted and many former sites have been drained or planted for forestry. There is therefore a limited amount of suitable habitat remaining for this unique combination of uncommon, rare or narrowly distributed species and this must be considered in future land use decisions.

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4 The relationship between taxonomic richness and pool area

4.1 INTRODUCTION

One of the most fundamental questions that can be asked in ecology is how many species can occur within a given area. A positive relationship between species richness and area has been reported in the literature so frequently that it is often regarded as "one of community ecology's few genuine laws"; a phrase first coined by Schoener (1976) and frequently referred to since (Connor & McCoy, 1979; McGuinness, 1984a; He & Legendre, 1996; Weiher, 1999; Lomolino, 2000). It is probably more accurately described by Holt *et al*. (1999) as "one of the most robust empirical generalisations in ecology". A number of mathematical formulae have been proposed which describe the increase in number of species with area although the exact nature of this relationship is subject to much discussion. Some dispute remains over the underlying mechanisms that generate a species-area curve, and the equation(s) that best describe it, possibly suggesting there is no single model to fit all data and no single process responsible.

Although scientists had previously noticed that the number of species observed increased with area (see reviews by Connor & McCoy, 1979; Rosenzweig, 1995), the relationship was not described mathematically until Arrhenius (1921) developed what is now known as the power function model (MacArthur & Wilson, 1963; 1967):

$$S = C A^Z,$$

where S = number of species, A = area and C and Z are constants. This relationship can be represented by the simpler, double logarithmic transformation (Connor & McCoy, 1979):

$$\log S = Z \log A + \log C.$$

Arrhenius (1921) tested his model empirically using plant communities and concluded that his formula was appropriate. An extended model of the power function has recently been published for the purposes of predicting large-scale species diversity from small-scale samples more accurately (Plotkin *et al.*, 2001).

An alternative model was proposed by Gleason (1922) after concluding the power function model was incorrect, finding that it greatly overestimated the number of species when extrapolated to large areas (although sampling intensity often decreases at large areas and therefore species numbers can be under-estimated in field observations). He proposed an exponential, or semi-log, relationship:

$$S = Z \log (A) + C$$

to describe the increase in number of species with area, which receives some support from plant ecologists (see Connor & McCoy, 1979; McGuinness, 1984a).

Some years later, another model, the logistic curve, was proposed by Archibald (1949) to estimate species richness in plant communities:

$$S = B/(C + A^{-Z})$$

where B is a constant. Although it is claimed that this model gives a considerably better fit when sampling large areas (He & Legendre, 1996) it has for some reason received little attention for either ecological or conservation purposes. This is possibly due to adequate fits being found using the simpler power or exponential models.

In addition to the mathematical formulae proposed to describe the relationship between species and area, many attempts have been made (and are still being made) to discover and explain the processes responsible for the relationship. When Arrhenius (1921) proposed his power function to predict the number of species in a given area, he also attempted to explain the processes involved. He proposed the random placement model, later called the passive sampling model (Connor & McCoy, 1979), which assumes that all individuals in the community are located at random. Any observed relationship between number of species and area is a result of random colonisation with smaller areas receiving fewer colonists and therefore fewer species (Arrhenius, 1921; Connor & McCoy, 1979; Coleman, 1981). The chance of finding a species is therefore a function of the size of the sample and the number of individuals of that species in the community. This relationship is also shown by Fisher, Corbet & Williams (1945). This model was supported by Coleman *et al.* (1982) who studied the variation in the number of breeding bird species on islands in Pyamtuning Lake on the Pennsylvania-Ohio border. Observed species richness varied with island size consistently with that expected if the birds were distributed randomly, with the probability of a breeding pair residing on an island being proportional to island size and independent of the presence of other pairs. The power function and the exponential models gave poorer fits to the data than the expected species-area curve based on the theory of random placement (Coleman *et al.*, 1982). In most areas or communities, however, it is unlikely that species are distributed at random due to the effects of local mechanisms such as competition or microhabitat preference, for example. The random placement theory did not account

for observed differences in numbers of arthropod species present among small mangrove islands (Simberloff, 1976).

An important explanation of one aspect of the species–area relationship was made by Williams (1943) using flowering plant species. He noticed that as soon as a certain size threshold was passed (approximately 0.01km^2) "new ecological conditions" began to be included in the sampling area resulting in a more rapid increase in the number of species than would be expected if conditions and populations remained uniform. It seemed that the species-area relationship for this part of the curve was related to an increase in the number of habitat types, with each new habitat type supporting new species. This explanation was later named the 'habitat diversity hypothesis' (Connor & McCoy, 1979). Williams (1943) found that the first part of his curve was best fit by the exponential model and the second part, once a given area had been reached and new types of habitat began to be included, by the power function model. Williams (1943) concluded that a significant fit of the power function model indicated a response to an increase in microhabitat diversity. Later, McGuinness (1984a) showed that the power function model alone provided a better fit to Williams' data than a combination of the exponential and power function models and, therefore, the whole of the curve, according to Williams' (1943) interpretation, could be explained by the habitat diversity hypothesis.

The habitat diversity hypothesis has been used to explain species-area curves in many subsequent situations where an increase in habitat diversity occurs (Maguire, 1971; Kodric-Brown & Brown, 1993; Douglas & Lake, 1994; Ricklefs & Lovette, 1999; Fox & Fox, 2000). Rosenzweig (1995) also provides a good review of this hypothesis. Although not actually fitting a curve to his data, Svenning (1999)

found more species in areas with increased microhabitat diversity. In a study on phytotelmata, Maguire (1971) found that size of the phytotelm alone (or its experimental equivalent – beakers filled with distilled water) was not an indicator of species richness. Although there was high species turnover in the water-bodies, he concluded that variation in the equilibrium number of species resulted largely from variation in habitat heterogeneity, not from the size of the phytotelm or the volume of water it contained. A conclusive report of increased habitat complexity resulting in increased species richness was shown in an experiment on fauna dwelling on natural and artificial stream stones (Douglas & Lake, 1994). Habitat diversity in the form of grooves on stones appeared to be a strong contributing factor for increasing species richness, independently of area. In a study of mammals on habitat islands, area and isolation, habitat diversity, habitat disturbance, species interactions and guild assembly rules were all tested as determinants of species richness (Fox & Fox, 2000). Habitat diversity was found to be the best predictor of species richness.

Some species-area relationships have been described, however, that do not support this hypothesis or that cannot be explained by habitat diversity alone. Ricklefs and Lovette (1999) found that habitat diversity effects were likely in highly specialised taxa and large populations which were less vulnerable to stochastic extinction but in taxa such as bats, which were less specialised and maintained low populations, an effect of area alone was more likely to occur. In his work on arthropod fauna in mangrove islands, Simberloff (1976) found that species richness increased with island size independently of habitat diversity. Although the habitat diversity hypothesis could not be applied to this system, Simberloff (1976) did not, however, discredit the hypothesis for other systems.

The next explanation for the species-area curve came from MacArthur and Wilson (1963; 1967). They proposed the equilibrium theory, later named the area *per se* hypothesis by Connor and McCoy (1979), which can be fitted by a power function curve. This theory attributes the number of species on an island to be the consequence of a 'dynamic equilibrium' between immigration and extinction. The number of species on an island remains constant but is 'dynamic' due to a continual turnover of species taking place *via* immigration and extinction. According to the theory, species richness on small islands will be lower due to smaller populations and an increased probability of extinction. This is supported by Hanski (1986) whose results of a study on shrews suggest that populations on small islands have high extinction rates. Conversely, equilibrium theory states that larger islands support larger populations which are less vulnerable to extinction (MacArthur & Wilson, 1963; 1967). Additionally, islands that are a long way from the main species pool or source will harbour fewer species than islands that are close. Theory predicts that the slope of the species-area relationship (using a power function model) will be steeper for islands closer to the main species source, or mainland, than those more distant.

This theory can be applied not only to oceanic islands but to many 'island' systems where similar habitat types are separated in space by relatively unfavourable habitats. For example, mountain peaks separated by valleys, water bodies separated by land, patches of woodland surrounded by urban developmensts, or even intertidal boulders separated by sand or pebbles can be considered as ecological islands. There has, however, been criticism of the theory and particularly the way it has been tested (Connor & McCoy, 1979; McGuinness, 1984a). There is some dissatisfaction that a

significant fit of the power function model is considered sufficient evidence to support the theory (Williamson, 1989).

The hypotheses mentioned so far have received much attention in the literature. Other explanations have been proposed that have received less attention, but may still be considered as possible mechanisms involved in generating species-area curves, or parts thereof. One such hypothesis which has been proposed but has received little attention in this context, is based on the intermediate disturbance hypothesis (Connell, 1978) and is discussed by McGuinness (1984a; 1984b). This hypothesis is more commonly used to describe species richness over a gradient of increasing disturbance, where species diversity is highest at an intermediate level of disturbance; the most frequently disturbed communities contain only the most tolerant species or early colonists, and communities with low disturbance are dominated by a few good competitors (Connell, 1978; Sousa, 1979; Townsend, Scarsbrook & Doledec, 1997). The intensity of a physical disturbance particularly, may be inversely proportional to area (Osman, 1977; Sousa, 1979; McGuinness, 1984b) which McGuinness (1984a; 1984b) suggests may predict a species-area curve. Evidence exists to support the hypothesis that the effects of increased disturbance on small areas does reduce diversity. This effect was shown in studies of waves on intertidal boulders (Sousa, 1979), small wave-washed cays in the Bahamas (Morrison, 1997) and in a study of mammals on habitat islands and isolates (Fox & Fox, 2000). However, there is little support for this hypothesis in large areas where reduced disturbance predicts a decrease in diversity. Disturbance events may be important in reducing diversity at the lower end of a species-area curve but other

mechanisms, such as an increase in habitat diversity, are likely to counteract the decrease in species richness with area that is predicted by disturbance theory.

Evolutionary factors, such as phylogenesis, have been proposed as influencing species richness on islands (Heaney, 2000) and it has been suggested that, on large islands, higher speciation rates may drive species-area relationships (Rosenzweig, 1975; Losos & Schluter, 2000; Lomolino, 2001). In a study of lizards on Caribbean islands (Losos & Schluter, 2000), above a threshold of island size, species richness increased at a greater rate primarily due to the positive effect of area on speciation rate. Another evolutionary effect was shown in a study of Aegean-island land snails (Welter-Schultes & Williams, 1999). The authors concluded that the unusually high species richness they found was relictual rather than due to the commonly proposed equilibrium theory. The largest island being studied had been at least six smaller islands for 7–9 million years during the Neogene period. The united island supported many endemic species of the palaeoislands causing species richness to be higher than that expected due to equilibrium theory.

The pools used in this study are not large or isolated enough to provide the geographic isolation necessary for *in situ* speciation to occur (Losos & Schluter, 2000; Heaney, 2000). Neither do the pools selected receive any regular disturbance from which the larger pools might provide a higher level of refuge (it is possible that the whole water column in very small, shallow pools may freeze in winter or dry up in summer, which may reduce species richness, but very shallow pools were not selected for this reason; disturbance/permanence is not the variable being tested). A relationship between species and area could therefore be generated by two other mechanisms in the pool complex at Forsinard. Firstly, species richness may increase

directly, as an effect of island area *per se.* A larger area will support larger populations, which are less likely to become extinct than small populations (MacArthur & Wilson, 1967) and larger pools make larger targets for potential colonisers. Secondly, the number of species may be affected by a factor that arises as a consequence of area: increased microhabitat diversity. However, because microhabitat diversity appears to be similar between all pools, any variation in species richness along the size gradient is likely to be a direct consequence of area, or more exactly, of the amount of space available. Another possible explanation for an increase in the number of species with area, greater sampling effort in large areas (Gleason, 1922; Arrhenius, 1923; Connor & McCoy, 1979), was controlled for in this study because, for the purposes of statistical analysis, sampling intensity is standardised across all pools.

In addition to looking at the response of all species to an increase in area, Holt *et al*. (1999) report some studies which have focused on species-area relationships between taxa varying in trophic rank. They present a model that predicts, when most consumers are specialists, species-area relationships should be stronger at higher trophic levels and they give some examples in which species-area relationships were examined for the effect of taxa at differing trophic ranks. There was some evidence that the slope *Z* was steeper at higher trophic levels.

Species-area relationships have received much attention in the literature because, despite being one of the few 'rules' in ecological theory, the exact nature of the relationship often differs between studies (or is even non-existent) and the suggested processes involved are highly variable. Determining the nature of the

relationship, and particularly the processes involved, is still the subject of much research.

Deriving species-area relationships can also have a more direct application. They can be used to determine the optimal size and number of samples needed to find all, or nearly all, the species in a system. For conservation purposes, they can be used to estimate the minimum area requirements of a 'community'. This is of particular importance to conservationists wishing to create protected areas and, conversely, for estimating species loss with habitat destruction. Kinzig and Harte (2000) proposed an endemics-area relationship, a modification of the species-area relationship that improves estimates of species extinction due to habitat loss. Species-area relationships are also used to extrapolate the number of species that can be expected in areas larger than those that were sampled, although care must be taken here as, in real systems, the slope *Z* may differ.

Although still a matter of some contention, species richness has sometimes been shown to increase stability in ecosystems (Tilman, 1996; Ives, Klug & Gross, 2000; Petchey, 2000; Borrvall, Ebenman & Jonsson, 2000; Cottingham, Brown & Lennon, 2002) although this may be dependent on how 'stability' is measured (Tilman, 1996). Species richness has also been shown to be important in determining the rate of ecosystem processes such as leaf litter breakdown (Jonsson & Malmqvist, 2000; Jonsson, Malmqvist & Hoffsten, 2001) and productivity (Waide *et al.*, 1999).

Establishing the underlying mechanisms that help to create species-area relationships is an important issue as many processes can be monitored and managed accordingly. For example, in a system of ecological islands or fragmented patches, if

an increase in habitat diversity with area was determined as the mechanism responsible for creating a species-area curve, that system could be managed with respect to maintaining habitat diversity; the size of the fragments may be of secondary importance. In contrast, if the size of an island *per se* is the single most important variable in the number of species it supports, then this is the factor that must be considered if biodiversity on the island is of issue. As Simberloff (1972) and Connor and McCoy (1979) rightly point out and as I mention earlier, species-area curves, collectively and individually, are quite possibly influenced by more than one process. The hypotheses described above are not necessarily mutually exclusive.

4.1.1 Species richness and species density

In this chapter I test whether variation in the number of species found per pool, within a standard number of samples, is a function of area. Because of the delicate nature of the pools, and their location on a SSSI, it was impossible to exhaustively survey each pool until every species was collected. This would have involved a high level of repeated sampling, severely depleting the numbers of individuals in each pool (which may have resulted in me being banned from the site!). Therefore the use of the term 'species richness', cannot refer to the exact number of species that are present in a pool and is replaced with 'number of species' which refers to the number of species collected in a standardised number of samples per pool (species density). Numbers of species collected in the sampling methods employed are representative of the number of species in the pool and are comparable. They are used as a measure, or an indication, of species diversity per pool. This is comparable to a "type 3" relationship, described by Holt (1992) and Holt *et al*.

(1999) as "local species richness in a sample of defined size, among habitats or regions differing in area".

Large differences between species richness (actual number of species per pool) and species density (number of species per unit area/sample) can occur in heterogeneous habitats. As the habitat within an area becomes more heterogeneous, species will become more aggregated, therefore reducing species density within the aggregated patches even if overall species richness is high. A species-area relationship therefore may be detected in highly heterogeneous habitats even if species density does not increase with area. In this study, two different microhabitat types (water column and pool bottom) were sampled using different sampling methods. From a visual inspection, each microhabitat type appeared homogenous within each pool, and species were therefore unlikely to be highly aggregated within each microhabitat type. Species density is therefore, although different to absolute species richness, an acceptable measure of species diversity in these pools.

In a study on the effects of forest fragmentation on spider communities (Miyashita, Shinkai & Chida, 1998), both species richness (total number of spider species found in each fragment) and species density (number of spider species per standardised sampling unit) displayed a significant, positive relationship when regressed against fragment area. A study of plant species diversity on true islands (Kohn & Walsh, 1994) found similar, positive relationships between species richness and island area, and species density and island area although the nature of the slope, particularly the gradient and R^2 values, differed. This suggests species density can be used as an indicator of relative species richness when determining the existence of a species-area relationship. The mathematical nature of a curve determined using

species density will almost certainly differ from the true species-area curve and the two should not be confused.

Confounding factors such as variations in microhabitat diversity amongst pools or differences in water chemistry are minimal, as reported in Chapter 3. Each pool can be considered as an ecological island where a discrete body of water is surrounded by land. The main difference between the pools is their size. Because microhabitat diversity is similar in all the pools sampled, I am able to test whether a simple increase in pool size (pool area) is responsible for an increase in number of taxa found. Both the power function (double-log) and the exponential (semi-log) models are fitted to the data. Species exhibit different behavioural and ecological responses to many variables and invertebrates at different trophic or taxonomic levels may show different responses to an increase in pool area. In addition to testing for an effect of area on the number of all taxa found in a pool, the numbers of taxa per pool within different trophic and taxonomic groups are also investigated.

4.2 METHODS

The three different sampling methods used (baited and unbaited activity traps, and sediment samples; see details in Chapter 3) were treated separately for the purposes of statistical analysis. Each data set comprised 22 pools sampled on four occasions at six-weekly intervals between April and September 1999. The log of the number of taxa per pool was regressed against the log of pool area (the power function model) for each individual sampling month, and then for all months combined, which increased the number of samples per pool. This was carried out separately for each of the three different sampling methods. Where there was a

significant effect of area on the number of taxa found using the power function, the semi-log model was fitted to see which gave the most significant fit. Where a significant fit was found in more than one sampling month, the number of taxa found per sampling unit was correlated with the number of individuals per sampling unit to test for an effect of abundance.

Some taxa could not be identified to species level, therefore the term 'taxa' is used rather than 'species'. Larvae of *Dytiscus* cannot be identified beyond the genus level in these pools and were allocated to the most abundant and widespread species, *Dytiscus lapponicus.*

4.2.1 Activity Traps

Baited activity traps consisted of traps placed in the water column (WCs) and traps which were allowed to sink until they rested on the pool bottom (Sinkers). Two baited activity traps were placed in each pool, one WC and one Sinker, and left for twenty-four hours. The cumulative number of taxa collected in both traps was then counted for each pool. The number of taxa was regressed against area, firstly for each sampling month and subsequently for all sampling months combined. Due to missing samples, Pool 1 (8.59m^2), Pool 7 (31.64m^2), Pool 9 (53.52m^2), Pool 15 (100.39m^2), Pool 16 (105.08m^2) and Pool 19 (142.97m^2) were excluded from the combined months analysis as only 3 months' data were available. Sixteen pools were therefore used in the regression analysis for number of taxa found in baited traps when all sampling months were combined.

Unbaited activity traps also consisted of WCs and Sinkers. Small pools contained one WC and one Sinker trap, medium pools two WC and one Sinker trap

and large pools three WC and two Sinker traps (see Chapter 3 for an explanation of pool-size categories). Taxa caught in the different trap positions (WC or Sinker) may differ; therefore each trap position was treated independently.

Initially, all unbaited activity traps in all sampling months were combined for each pool and the cumulative number of taxa calculated. The number of taxa for each pool was then regressed against pool area. However, because of the scaled sampling method, larger pools have more samples. To obtain a comparable count of taxa found in each pool, a standardised number of traps were combined for each pool and the cumulative number of taxa calculated in each set of traps. The maximum number of traps that could be selected so that an equal number was used from each pool was one WC and one Sinker (a 'trap-pair'). In the small pools where there was only one of each trap type, those traps were selected each time and the number of taxa calculated. In the medium and large pools all possible combinations of one WC and one Sinker were selected for each pool and the number of taxa calculated for each trap-pair. The mean number of taxa per trap-pair was then calculated from all sets of possible trap-pairs for each pool. Regression analysis was carried out on the mean number of taxa to test for an effect of pool area, for each separate sampling month.

To increase the sample size in the unbaited traps, data were combined over all sampling months. The cumulative number of taxa found per four trap-pairs (one random selection from each sampling month) for each pool was then calculated. In the small pools where only one trap-pair was available per month, that trap-pair was used each time. The selection process of four trap-pairs per pool, and subsequent regression analysis of each set of data against the pool size gradient was carried out

ten times. Although this is an arbitrary number of data sets on which to perform separate regression analyses, I deemed this sufficient to obtain a reliable determination of the effect of area on taxon density found in each pool. For each set of the ten data sets, the log of number of taxa per four trap-pairs was regressed against the log of pool area. Due to missing samples, Pool 2 (13.28 m^2), Pool 3 (14.06 m^2), Pool 5 (29.30 m^2) and Pool 11 (59.77 m^2) were excluded from the analyses as only 3 months' data were available. Eighteen pools were therefore used in the regression analysis when all months were combined.

4.2.2 Sediment samples

Sediment samples were collected as detailed in Chapter 3; one sample was taken from the small pools, two from the medium pools and three from the large pools on each of the four sampling occasions during 1999. Initially, each sampling month was considered separately. As with the unbaited activity traps, if more taxa were found in the larger pools in an unbalanced design the possibility of the result being a factor of sample size could not be ruled out. Therefore, the number of taxa in only one sample per pool was calculated for each of the four sampling months. In pools with more than one sample taken per month, one sample was randomly selected from each pool, for each sampling month. This random selection process was carried out ten times, thus there were ten data sets for taxon density with pool area for each sampling month. In the small pools where only one sample was taken per sampling month, that sample was used in each data set. The affect of pool area on taxon density was tested using regression analysis. Analysis was carried out separately on each of the ten data sets for each month.

To include more samples per pool, sampling months were then combined. The cumulative number of taxa found per four samples (one randomly selected from each sampling month) for each pool was then calculated. In the small pools where only one sample was available per month, that sample was used each time. The selection process of four samples per pool, and subsequent regression analysis of each set of data against the pool size gradient was carried out ten times. Due to missing data, Pool 3 (14.06m^2) and Pool 21 (253.91m^2) were excluded from this analysis as only 3 months' data were available.

4.2.3 Taxonomic and trophic groups

In addition to testing for an effect of area on the number of all taxa in each pool, diverse taxonomic and trophic groups were also investigated for a response to an increase in pool area. In the baited and unbaited activity traps the diverse taxonomic groups were diving beetles and microcrustacea, and trophic groups were herbivores, predators and 'others' (see Chapter 3 for definitions). In the sediment samples the only diverse taxonomic group was the Chironomidae; diverse trophic groups were predators and 'others'. A taxon may therefore appear in two groups e.g. beetle *X* will be included in both the diving beetle group and the predator group but, as groups are not being compared directly, the statistical analysis will not be affected. In the sediment samples, regression of 'others' was unnecessary as thirteen out of sixteen chironomid taxa were detritivores (categorised as 'others'). Sediment samples contained no herbivores. The numbers of taxa per taxonomic or trophic group were calculated along the pool size gradient for each separate sampling month

and then for all months combined using the same methods as above. The different sampling methods were analysed separately.

4.2.4 Random sampling

Where samples were selected for purposes of statistical analysis, a specially written selection program was written (C.J. Legg, unpublished) using Delphi software. For the unbaited activity traps, the program firstly selected every combination of 1 Sinker trap and 1 WC trap per pool per sampling month. These data were then used to find the mean number of taxa per trap-pair per pool for each sampling month. The program then randomly selected one trap-pair from each pool for each month, which were combined and used in the 'all months' analysis. There were thus four trap-pairs used to calculate the number of taxa found per pool. For analysis of the sediment samples, the program selected one sample per pool for each of the four sampling months. These were analysed by month or combined so that, for each pool, there were four samples used in the 'all months' analysis.

Due to the similarity in results of the regression analyses among each data set, I deemed ten random combinations of samples to be sufficient to obtain a reliable indication of the effect of pool size on taxon density.

4.2.5 Statistical analysis

A power function (Arrhenius, 1921; Connor & McCoy, 1979) was initially fitted to each data set to test for the effect of area on the number of taxa found. Where a result was significant ($P \leq 0.05$), Gleason's (1922) exponential function was also fitted to establish which model gave the best fit. The power function and exponential models were represented by double-log and semi-log transformations

respectively (Connor & McCoy, 1979). The beetle data included zero values for several pools and these data were therefore transformed log (x + 1), as appropriate. All other data, where transformed was transformed log (x). All data were tested for a normal distribution. Simple linear regression was carried out on all transformed data sets using Minitab 12 software.

4.2.6 Sample effort curves

Sample effort curves were plotted to address how effectively a small number of samples (that used to calculate species density) capture taxa compared to the maximum number of samples taken from a single pool. A specially written programme (C.J. Legg, unpublished), using Delphi software, calculated the mean number of taxa per sampling effort. These numbers were then used to plot mean species accumulation curves for each pool, firstly combining samples from all four sampling dates and secondly for each separate sampling month. Sample-effort curves were plotted for unbaited activity traps and sediment samples only. The number of baited activity traps for each pool was standardised, therefore effort was equal in all pools making sample-effort curves unnecessary.

Curves were firstly plotted using data from only the largest pools in order that the number of samples used to calculate taxon density (8) can be compared with the largest number of samples taken (20). A second and third set of curves were also plotted, each using data from two small pools (maximum 8 samples), two medium pools (maximum 12 samples), and two large pools (maximum 20 samples) to compare accumulation curves over a wider range of pool sizes. These curves were plotted on two figures, rather than one, to avoid crowding the figure and to observe

several different pools. The total number of samples for each pool may differ slightly due to missing data.

4.3 RESULTS

4.3.1 Number of all taxa (taxon density)

For each sampling method, all traps or samples per pool for all sampling months were combined and the cumulative number of species per pool was calculated (Figure 4.1).

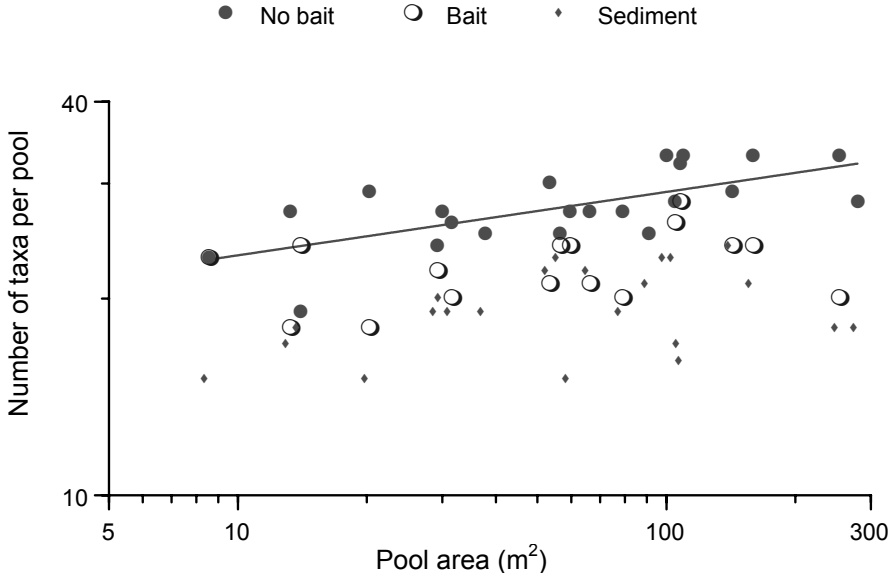

Figure 4.1. Overall number of taxa per pool for all months combined plotted against pool area (logarithmic scales). For unbaited activity traps and sediment samples the data is based on scaled sampling methods where more samples were taken from the larger pools. The fitted line shows a significant regression of unbaited activity traps.

There was no affect of area on the number of taxa collected in baited activity traps or in sediment samples. There was a significant affect of area (for both a power function and an exponential function, $R^2 = 0.42$, $P = 0.001$) for the number of taxa collected in unbaited activity traps. The results for unbaited activity traps and

sediment samples, however, were based on a scaled sampling method and there were more samples in the larger pools.

The following results present data which compare the same number of traps per pool or the mean number of taxa per trap-pair.

Table 4.1. Results of regression analysis of log taxon density vs. log area for baited and unbaited activity traps. Taxon density is explained as no. of taxa per trap-pair for baited traps and mean number of taxa per trap-pair for unbaited traps. Log (x+1) used for beetles as counts included zeros.) R^2 values, slope, P-value and degrees of freedom (DF) are presented. * indicates a significant ($P < 0.05$) fit of the regression slope. NS indicates non-significant results for the 10 regression analyses carried out for number of taxa in unbaited activity traps over all months (see Table 4.3). Results of fitting the exponential function to significant results are shown in Table 4.2.

Taxonomic	**Baited traps**				**Unbaited traps**			
group	**R^2**	**Slope**	**P**	**DF**	**R^2**	**Slope**	**P**	**DF**
All taxa								
All months	0.05	0.04	0.21	15	-	-	NS	17
April	0.02	0.12	0.25	18	0.28	0.08	<0.01*	21
June	0.11	0.12	0.08	19	0.00	0.02	0.69	17
July	0.08	0.06	0.11	21	0.00	0.03	0.39	21
September	0.00	0.07	0.44	20	0.00	- 0.02	0.67	21
Diving Beetles								
All months	0.32	0.23	<0.01*	15	-	-	NS	17
April	0.30	0.22	<0.01*	18	0.03	0.09	0.22	21
June	0.22	0.28	0.02*	19	0.16	0.23	0.06	17
July	0.09	0.20	0.10	21	0.00	0.07	0.38	21
September	0.24	0.26	<0.01*	20	0.04	- 0.09	0.31	21
Microcrustacea								
All months	0.00	0.01	0.75	15	-	-	NS	17
April	0.00	0.08	0.48	18	0.28*	0.14	<0.01*	21
June	0.13	0.12	0.06	19	0.00	0.03	0.39	17
July	0.06	0.05	0.14	21	0.05	0.07	0.17	21
September	0.00	0.04	0.71	20	0.00	0.02	0.78	21
Herbivores								
All months	0.00	0.02	0.63	15	-	-	NS	17
April	0.01	0.12	0.29	18	0.28	0.11	<0.01*	21
June	0.21	0.15	0.03*	19	0.05	0.05	0.19	17
July	0.10	0.07	0.08	21	0.12	0.10	0.07	21
September	0.00	0.08	0.45	20	0.00	0.03	0.69	21
Predators								
All months	0.22	0.16	0.04*	15	-	-	NS	17
April	0.15	0.22	0.06	18	0.26	0.04	0.23	21
June	0.09	0.13	0.10	19	0.00	0.02	0.79	17
July	0.00	0.01	0.87	21	0.06	0.08	0.13	21
September	0.13	0.13	0.06	20	0.02	- 0.06	0.24	21
Others								
All months	0.00	- 0.05	0.38	15	-	-	NS	17
April	0.00	0.05	0.51	18	0.00	0.04	0.42	21
June	0.00	- 0.05	0.38	19	0.03	- 0.07	0.25	17
July	0.00	0.04	0.57	21	0.00	0.01	0.69	21
September	0.00	- 0.05	0.52	20	0.00	- 0.04	0.44	21

Firstly a power function model was fitted to the data. All R^2 values, slopes, P values and degrees of freedom for analyses on number of taxa collected in baited and unbaited activity traps, based on a standardised number of samples, are presented in Table 4.1. Results for analyses carried out on sediment samples are presented in Appendices 4.1 and 4.2. Where a fit of the power function was significant ($P < 0.05$), data were also regressed using an exponential model (Table 4.2) to see which model gave the best fit.

Table 4.2. Results of regression analysis of no. of taxa vs. log area for baited and unbaited activity traps. This semi-log model has only been fitted where the power function gave a significant ($P < 0.05$) result (see Table 4.1). R^2, slope, P, and degrees of freedom (DF) are presented.

Taxonomic	**Bait**				**No bait**			
group	**R^2**	**Slope**	**P**	**DF**	**R^2**	**Slope**	**P**	**DF**
All taxa								
April	-	-	-	-	0.27	0.08	<0.01	21
Beetles								
All month	0.36	2.26	<0.01	15	-	-	-	-
April	0.31	0.83	<0.01	18	-	-	-	-
June	0.24	1.40	0.03	19	-	-	-	-
September	0.26	1.23	0.01	20	-	-	-	-
Microcrustacea								
April	-	-	-	-	0.26	2.09	<0.01	21
Herbivores								
April	-	-	-	-	0.26	1.39	<0.01	21
June	0.18	2.49	0.04	19	-	-	-	-
Predators								
All months	0.22	2.42	0.04	15	-	-	-	-

Once scaled sampling effect had been removed from the unbaited activity trap data, there was no effect of pool area on taxon density when all sampling months were combined (Table 4.1). When taxon density was analysed for each separate sampling month, April was the only sampling month, for unbaited traps, where there was evidence of an effect of area on the number of taxa found (Figure 4.2). The double log-transformed data for April unbaited activity traps gave a slightly higher

R^2 value and a slightly lower P-value (Table 4.1) than the semi-log transformed data (Table 4.2). The number of taxa found in the June, July and September samples showed no detectable effect of pool area. For invertebrates collected using baited activity traps, no significant relationship (P >0.05) between pool area and number of taxa was found for any single sampling month.

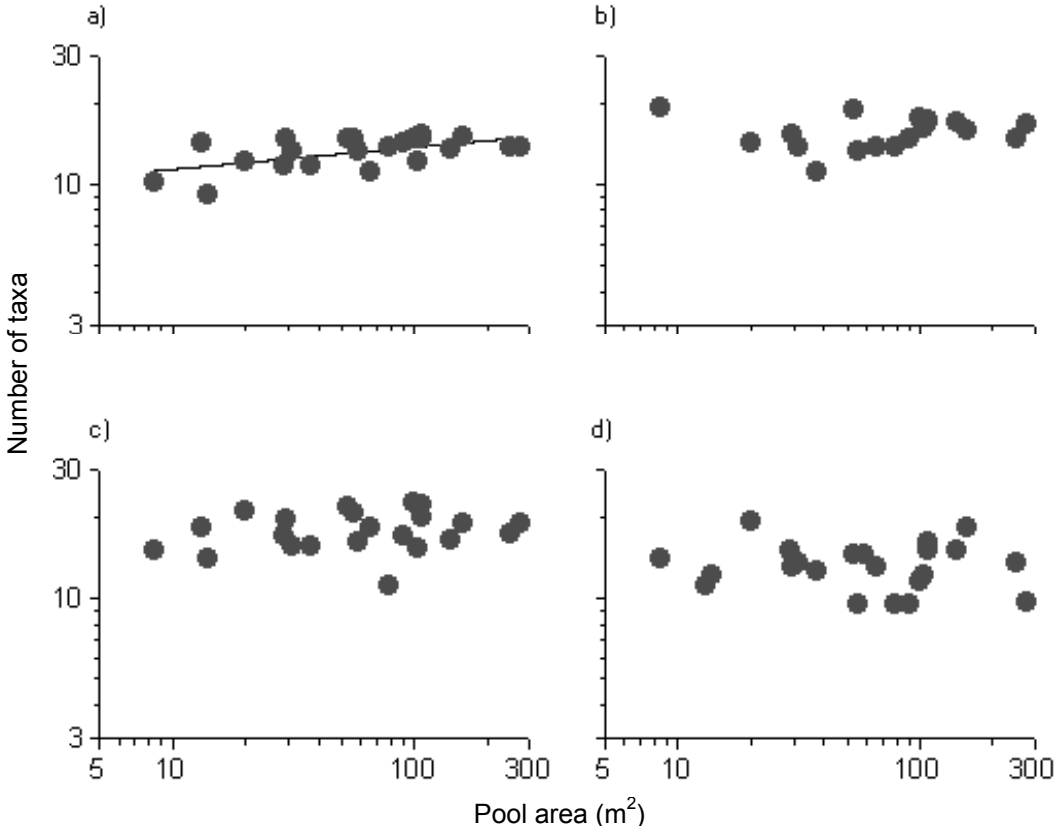

Figure 4.2. Number of taxa found per unbaited trap-pair (1 Sinker + 1 WC) plotted against pool area (logarithmic scales) for a) April, b) June, c) July and d) Sept 1999. Where there was more than one trap combination for each pool, the mean number of taxa per trap-pair was used (see Section 4.2). April was the only sampling occasion in which area had a statistically significant effect (P < 0.05) on the number of taxa found.

When the scaled sampling effect had been removed for invertebrates collected in the sediment samples, variation in taxon density remained independent of pool area for all four sampling months. This was consistent across all ten sets of randomly selected samples (max. R^2 = 0.02, min. P = 0.25, see Appendix 4.1). When all sampling months were combined (so four samples per pool were analysed) and the cumulative number of taxa found in each pool was calculated there was, again, no significant effect of area on number of taxa in any of the ten random selections of samples (max. R^2 =0.04, min P = 0.32, see Appendix 4.2).

4.3.2 Taxonomic and trophic groups

In the unbaited activity traps there was a significant effect of pool area in April for the number of microcrustacean taxa (Table 4.1, Figure 4.3) and herbivore taxa (Table 4.1, Figure 4.4) collected. When unbaited activity traps were combined over all months (with a standardised number of traps), diving beetles were the only group where the number of taxa per pool showed an effect of area, although this was for only one out of ten random selections of data (Table 4.3) and therefore the probability of a Type 1 error is high. In baited activity traps, there was an increase in the number of diving beetles taxa with pool area when all months were combined (Table 4.1, Figure 4.5) and in April, June and September (Table 4.1, Figure 4.6), for herbivores in June (Table 4.1, Figure 4.7) and for all predators when all months were combined (Table 4.1, Figure 4.8). In the sediment samples, there was no effect of pool size for any group.

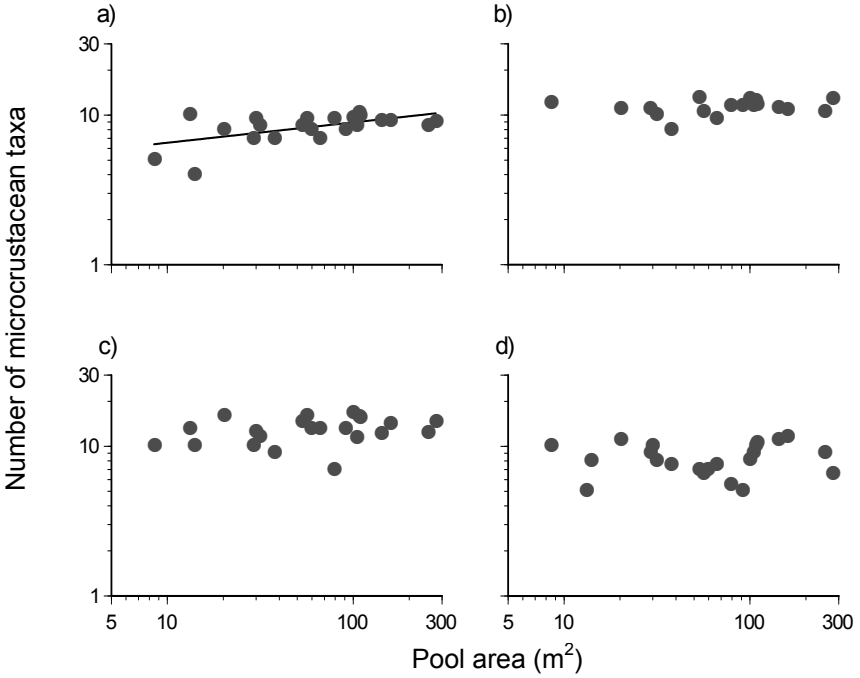

Figure 4.3. Number of microcrustacean taxa found per unbaited trap-pair (1 Sinker + 1 WC) plotted against pool area (logarithmic scales) for a) April, b) June, c) July and d) Sept 1999. Where there was more than one trap-pair for each pool, the mean number of taxa per trap-pair was used (see Section 4.2). The regression slope was significantly different from zero (P = < 0.05) for April only.

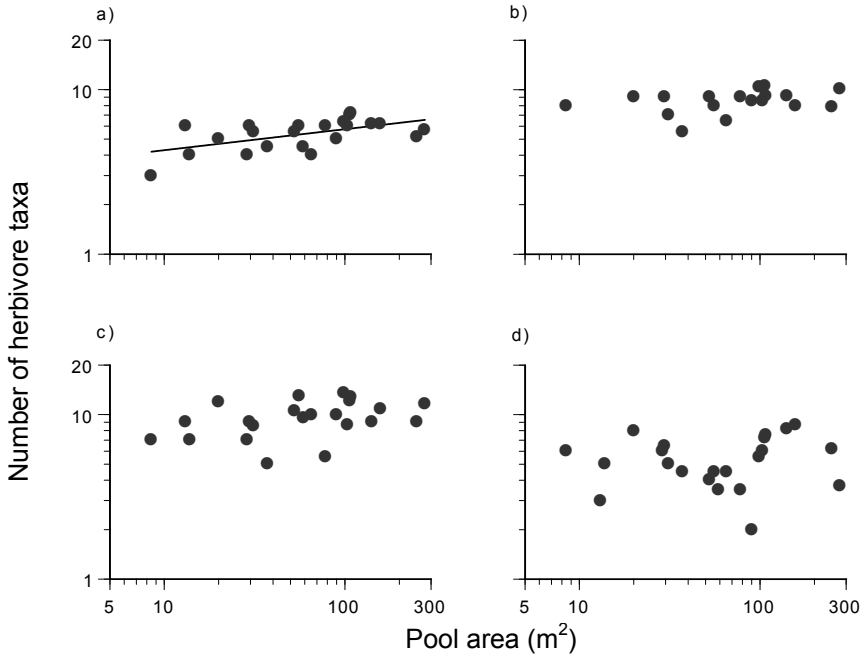

Figure 4.4. Number of herbivores found in per unbaited trap-pair plotted against pool area (logarithmic scales) for a) April, b) June, c) July and d) Sept 1999. Where there was more than one trap-pair for each pool the mean number of taxa per trap-pair was used (see Section 4.2). The regression slope was significantly different from zero (P = < 0.05) for April only.

Table 4.3. Results of regression analysis of log taxon density vs. log pool area for all months combined for unbaited activity traps. For each category, 10 regression analyses were carried out on randomly selected samples from each pool (see text). Maximum R^2, range of slopes and minimum P are presented. Degrees of freedom = 17 for all regressions carried out. Significant P is shown by *.

	Max R^2	Slope	Min P
All taxa	0.00	0.01 – 0.03	0.37
Diving beetles	0.18	0.08 – 0.25	0.04*
Microcrustacea	0.09	0.02 – 0.06	0.11
Herbivores	0.15	0.04 – 0.09	0.07
Predators	0.00	-0.04 – 0.02	0.38
Other	0.10	-0.09 – 0.01	0.11

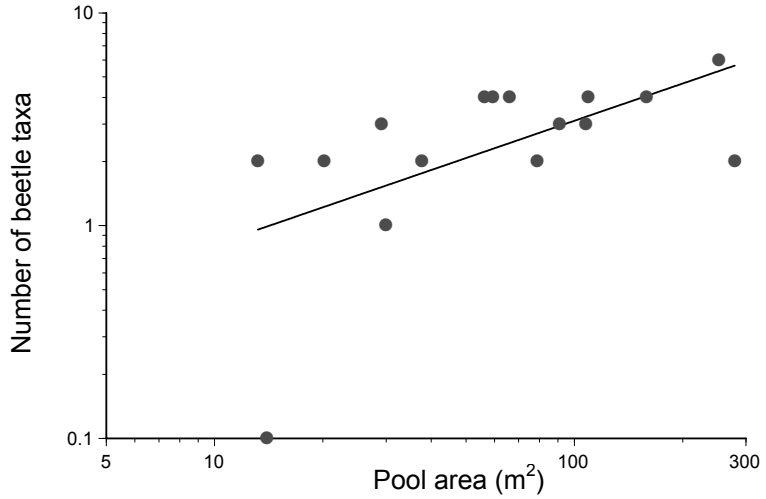

Figure 4.5. Number of diving beetle taxa caught in baited activity traps for all sampling months combined, plotted against pool area (logarithmic scales). Pools 1,7,9,15,16and 19 have been excluded due to missing data. The single zero data point is represented as 0.1 for illustrative purposes only and was included as a zero in the analyses. The regression line fitted is significantly different from zero.

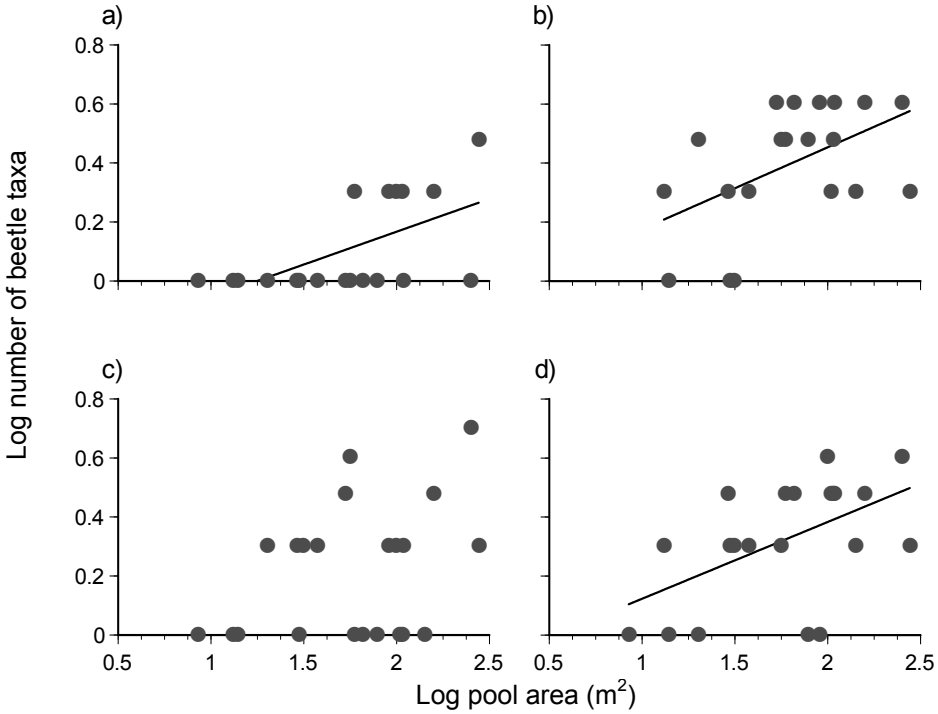

Figure 4.6. Log (x + 1) number of beetle taxa caught in two baited activity traps per pool for a) April, b) June, c) July and d) September 1999. Fitted regression slopes were significantly different from zero (P = < 0.05).

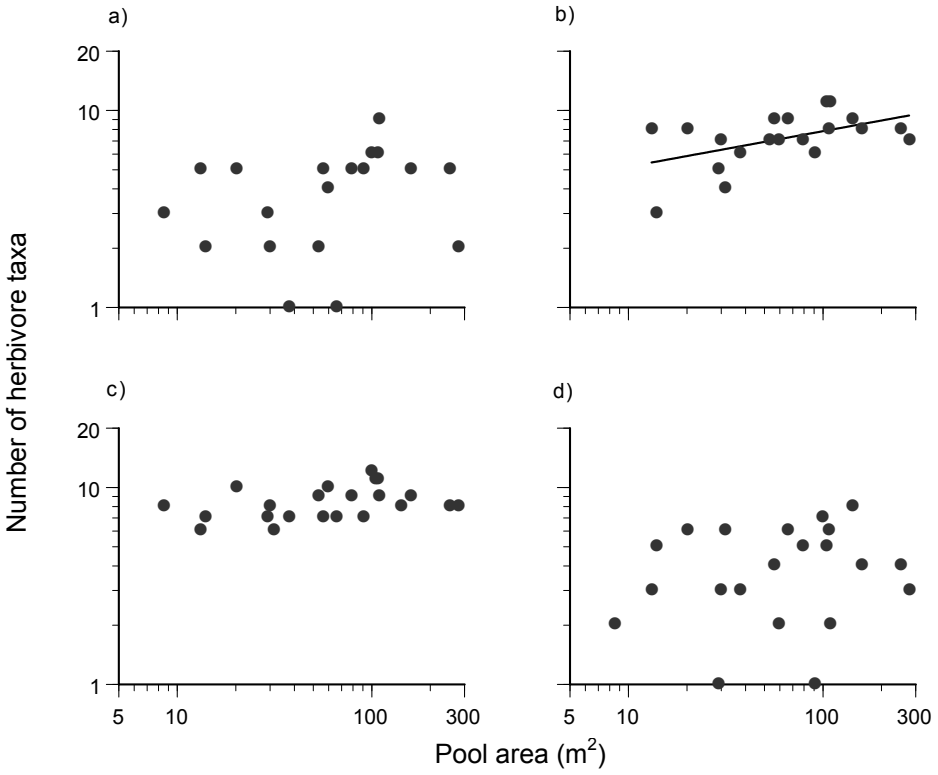

Figure 4.7. Number of herbivores found per two baited activity traps plotted against pool area (logarithmic scales) for a) April, b) June, c) July and d) Sept 1999. The regression slope was significantly different from zero (P = < 0.05) for June only.

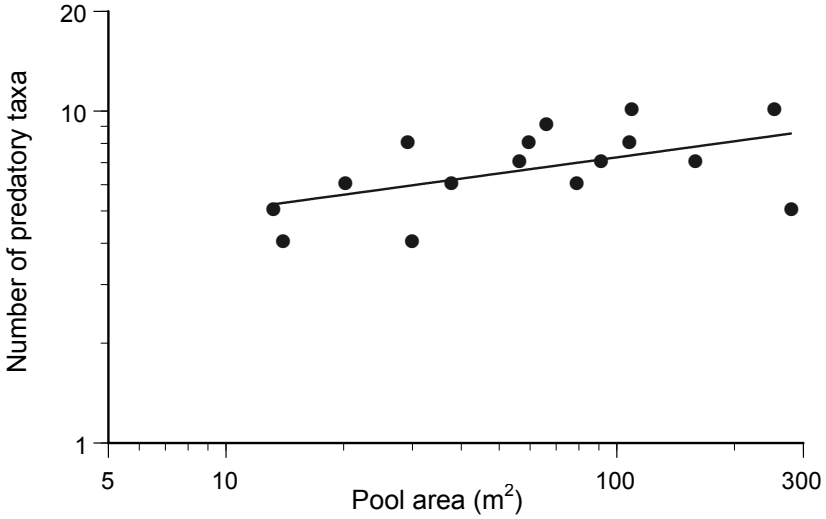

Figure 4.8. Number of predatory taxa caught in baited activity traps for all sampling months combined plotted against pool area (logarithmic scales). Pools 1, 7, 9, 15, 16 and 19 have been excluded due to missing data. The regression slope was significantly different from zero (P = < 0.05).

The power model gave a higher R^2 and lower P value than the exponential model for herbivores in June baited traps, and microcrustacea and herbivores in April unbaited traps (Table 4.1, Table 4.2). The R^2 was slightly lower although slightly more significant for beetles in June baited traps using the power model. Both the R^2 and P values were equal for both models in the regression of all predators in baited traps when all months were combined. The exponential model (Table 4.2) gave the highest R^2 and the lowest P values for diving beetles in baited traps in April, September and when all traps were combined. Although there is some overlap in the taxa included in the different groups, overall, there is a weak positive relationship throughout most of Table 4.1. All significant results have positive slopes, as do the majority of non-significant results. There are only eight negative slopes which all have low R^2 values (the highest is 0.04).

To test for a relationship between the number of diving beetle individuals on the number of diving beetle taxa in baited traps, Spearman's Rank correlation was

carried out on these two variables. This is the appropriate test to use when neither variable is fixed (Zar, 1999). Rank correlation was also carried out against number of individuals and pool area. Abundance data was non-normal and Spearmans' rank correlation was therefore the appropriate test. There was a significant correlation between the number of beetle taxa and the number of individuals for each sampling month and for all months combined (Table 4.4). As expected, there was also a significant correlation between the number of individuals and pool area for April, June, September and all months combined (Table 4.4).

Table 4.4. Results of Spearman's rank correlation for a) number of diving beetle individuals vs. number of beetle taxa and b) number of individuals vs. area per baited activity trap-pair (4 trap-pairs for all year data). * Indicates a significant relationship ($P < 0.05$). Pools of area 8.59, 31.64, 53.52, 100.39, 105.08, and 142.97m^2 were excluded from the 'all year' analysis due to missing data. r_s = correlation coefficient, N = sample size

	r_s	P	N
a) Taxa vs. individuals			
All year	0.743	<0.001*	16
April	0.982	<0.000*	19
June	0.909	<0.000*	20
July	0.958	<0.000*	22
September	0.820	<0.000*	21
b) Individuals vs. area			
All year	0.554	0.026*	16
April	0.608	0.006*	19
June	0.636	0.003*	20
July	0.253	0.257	22
September	0.703	<0.000*	21

4.3.3 Sample effort curves

In the plot of large pools (Figure 4.9), the number of taxa collected in 8 samples (the number of samples used to calculate taxon density) is consistently lower

than in the total number of samples taken (18 or 20). This is in accordance with the expectation that more samples will contain more species. However, the order of the curves at 8 samples is similar to the order of the curves at 20 samples. This indicates that some predictions of the rank order of pool taxon richness, can be made from 8 samples. Importantly, the height of the curves at any point along the x-axis show no relationship with pool size (indicated by pool number).

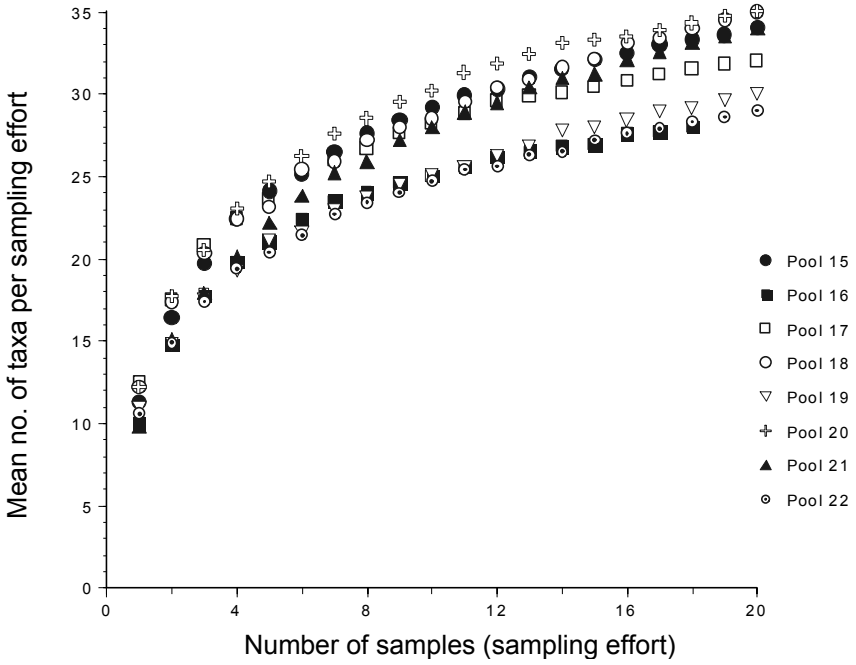

Figure 4.9. Mean sample effort curve showing number of taxa collected per number of sample used for large pools only. Samples are pooled across season and selected at random to calculate mean number of taxa per sampling effort.

In Figure 4.10, sample-effort curves for a range of pool sizes (two small, two medium and two large) show similar results to Figure 4.9. Eight samples contain

less taxa than 12 or 20 samples (the total number of samples collected in medium and large pools respectively) and, again, the relative heights of the curves at any point along the x-axis is not determined by pool size. The rate at which species accumulate is also independent of pool size.

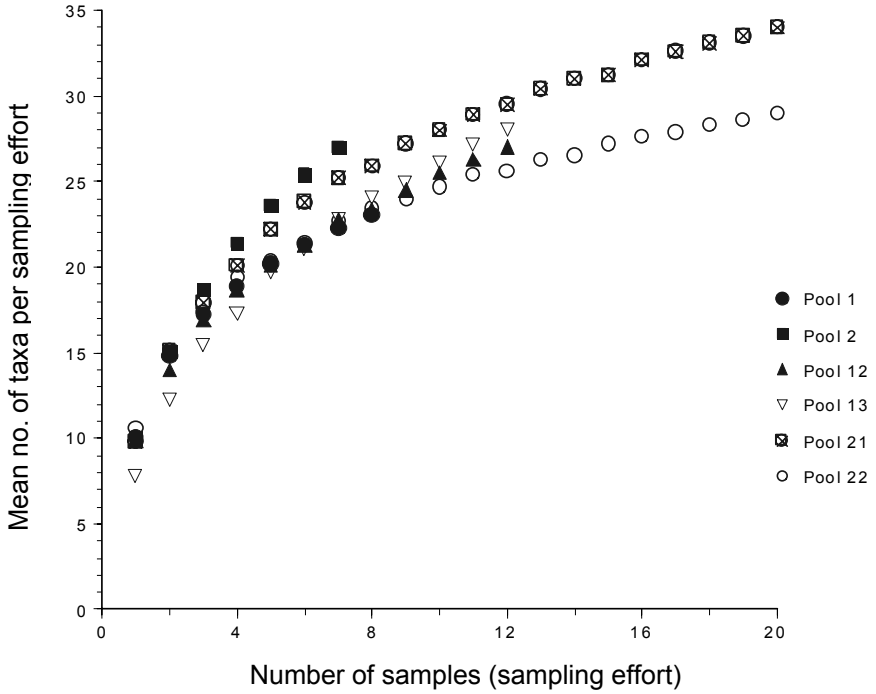

Figure 4.10. Mean sample effort curve showing number of taxa collected per number of sample used for the two smallest, two medium and the two largest pools. Samples are pooled across season and selected at random to calculate mean number of taxa per sampling effort.

Figure 4.11 shows a different set of two small, two medium and two large pools. Again, at eight samples the relative heights of the curve are similar to the relative heights at 12 or 20 samples, where applicable. Both the height of a curve at any one point along the x-axis and the acceleration rate of a curves are independent of pool size.

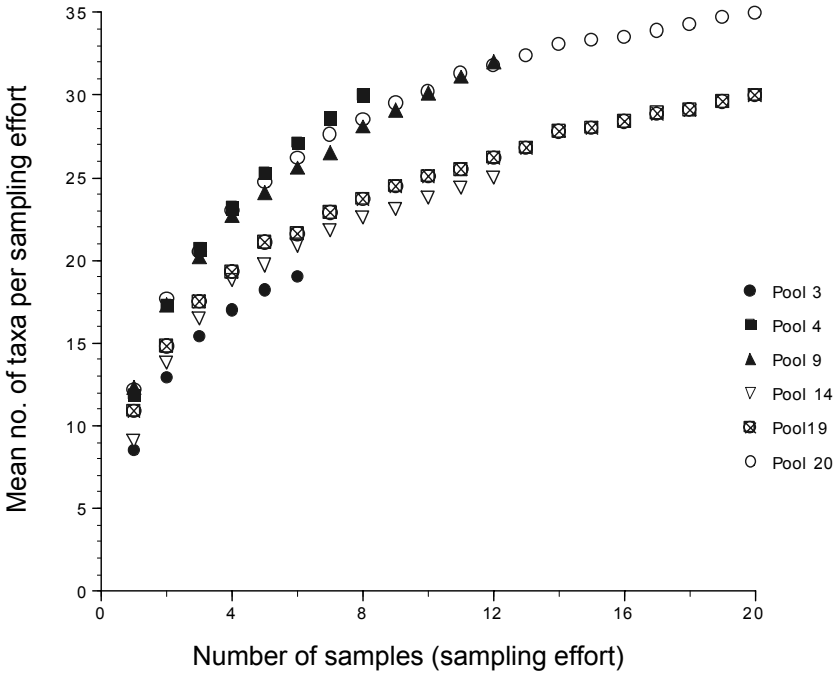

Figure 4.11. Mean sample effort curve showing number of taxa collected per number of sample used for two small, two medium and two large pools. Samples are pooled across season and selected at random to calculate mean number of taxa per sampling effort.

For the sediment samples, preliminary analysis (Figure 4.1) shows that, even when more samples are taken from the larger pools (i.e. more sampling effort), there is no relationship between number of taxa collected and pool size/sampling effort. Similarly, sample-effort curves show no relationship for sediment samples and are not therefore shown.

4.4 DISCUSSION

4.4.1 Number of all taxa per pool

The pools in this study were chosen to represent ecological islands with each discrete body of water being separated from the next by uninhabitable terrestrial habitat. For each separate sampling method, when all taxa were considered within a standardised number of samples, only the unbaited activity traps in April showed an effect of area on the number of taxa collected per standardised sampling unit. This is only weak evidence that the larger pools contain more taxa than smaller pools; given the number of analyses performed, this may have arisen due to a Type 1 error. This suggests that either a species-area relationship cannot always be detected on ecological islands and that other factors affect the number of species found or, that the pool were insufficiently isolated to act as ecological islands. Alternatively, the detection of a species-area relationship may be seasonal in this system; this is discussed later.

Lomolino (2000) states that different mechanisms may apply to different parts of the species-area curve and that data may fluctuate about the initial part of a curve due to the 'small-island effect' (where species richness is independent of area). Small island effects have previously been reported in several species-area relationships (e.g. Niering, 1963; MacArthur & Wilson, 1967; Whitehead & Jones, 1969; Heatwole & Levins, 1973; Morrison, 1997; Lomolino, 2000). In this first part of a curve where area is small, factors such as habitat type (Whitehead & Jones, 1969), disturbance (MacArthur & Wilson, 1967; Morrison, 1997), isolation and interspecific interactions (Morrison, 1997; Whittaker, 1998; Lomolino, 2000) are more likely to determine species richness than area. Alternatively, smaller islands

may be disproportionately subsidised energetically by allochthonous input from the surrounding matrix due to a smaller middle:edge ratio (Anderson & Wait, 2002). Thus, increased available nutrient resources may result in increased species richness *via* higher population densities and lower extinction rates.

Small island effects have been reported at many different scales ranging from islands up to 300 m^2 for vegetation on Bahamian cays (Morrison, 1997) to areas up to approximately 250 $miles^2$ for ponerine ants on oceanic islands (Wilson, 1961). Although the fauna in this study are small, the pools may be within the range of areas (9 – 281 m^2) sensitive to the small island effect. Within this range, pools increase in size but not in habitat diversity; each microhabitat type just gets bigger. Until the pools reach a size where microhabitat diversity increases, there may be no effect of area on the number of species in a pool. Heatwole and Levins (1973) report such a phenomenon where an increase in area of sand cay islands added more of the same habitat; species were restricted to those adapted to that one habitat.

The close proximity of the pools to one another is likely to be a highly important factor in determining the persistence of invertebrate species populations *via* the rescue effect (Brown & Kodric-Brown, 1977). This is the effect of small populations being 'rescued' from extinction by recolonisation from nearby populations (Ricklefs & Cox, 1972; Brown & Kodric-Brown, 1977; Ricklefs & Lovette, 1999). All the insect taxa in the study pools have an aerial adult stage, during which oviposition by females may take place in pools other than that from which the adult female emerged. Scaled to the whole pool complex, it is reasonable to assume that emerging females can oviposit in any pool in the complex, depending on their flight capabilities, and multiple 'rescues' of small populations at risk of

extinction can take place on an annual basis. The rescue effect has been suggested in butterfly populations on islands in the Lesser Antilles of the Caribbean (Ricklefs & Lovette, 1999) where vagility of the adults is high and island area was found not to be a good predictor of species richness. On analysing the same data, Morand (2000) noticed that species richness in birds, bats and butterflies was related to distance between islands, whilst reptiles and amphibians were highly endemic to each island with species richness being unrelated to geographical distance. He concluded that high vagility between islands decreased the chance of extinction by enhancing the rescue effect. High vagility of the adult insects in this study may considerably reduce the effect of pool size on species occupancy. In artificial ponds in which numbers of predator and prey taxa were manipulated (Jeffries, 2002), predator:prey ratios converged over two years due to the spread of the augmented local species pool rather than to individual community level adjustment within each pond. A similar spread of species across the site may be determining species occupancy in the pools at Forsinard, independently of area.

The pools in my complex therefore, may not be isolated islands due to high levels of immigration from other pools. Even if females oviposit in the pool from which they emerge, mating with males from other pools can be considered a genetic rescue effect. Thus, the pool complex as a whole is likely to support a single population of the more vagile species rather than isolated populations in each pool: apparent barriers to migration are not barriers at all and, for insects at least, the whole complex may be a single patchy habitat. The insects are merely aggregated in pools during the aquatic stage of their life cycle. Therefore, the rescue effect may stabilise and converge pool assemblages by supplementing populations on a regular basis.

The rescue effect could be important for conservation purposes when applied to fragmented habitats. Provided some form of corridor is available which allows a rescue effect then small fragmented areas of similar habitat may be able to maintain a species richness comparable to a single larger area (Gilbert, Gonzalez & Evans-Freke, 1998; Gonzalez *et al.*, 1998). In a study of fragmented Australian forests (MacNally & Horrocks, 2002), rather than 'relax' due to isolation, avifaunal assemblages appeared to be dominated by recolonisation and abandonment. Density of individuals appeared dependent on corridors or linkages between fragments. In the study pools, the corridor takes the form of the adult flight period and the short distance between pools. For the microcrustacea, bird-mediated passive transport may act as a corridor and aid dispersal between pools (Maguire, 1963; Figuerola & Green, 2002; Cáceres & Soluk, 2002). Occasional high winds may also carry microcrustacea in spray between pools.

Due to the close proximity of the pools to one another (each <15 m from its nearest neighbour) and the rescue effect, the minimum area required to maintain a viable population of a species is reduced compared to that required by an isolated pool. The area required in the study pools is that needed to maintain a population of a particular species throughout its aquatic (larval) stage only (for insect species). For microcrustacea, even the smallest pool included in the study may be sufficient to maintain populations of most species. Pools would therefore have to be very small before an effect of area was noticed. Such pools would not be included in this study because they are very shallow and may therefore differ in their open-water microhabitat type from larger pools. Additionally, I could not be certain that such

small, shallow pools were permanent, or that they did not completely freeze in winter, thereby introducing confounding variables.

4.4.2 Taxonomic and trophic groups

The number of diving beetle taxa found in baited traps in April, June and September (per trap-pair) and when all sampling months were combined (per four trap-pairs) increased significantly with pool area. This effect was not found in the unbaited traps. The number of beetle taxa collected in baited traps also showed a significant positive correlation with the number of individuals collected, which increased with pool area for the same three sampling occasions as the number of taxa increased with pool area. There was no increase in the number of individuals caught in unbaited traps along the size gradient. Thus, it appears that the effect of pool area on the number of diving beetle taxa in the baited traps is a result of an increased sample size in the larger pools, despite sampling techniques being uniform throughout the range of pool areas. Diving beetles are highly mobile within a pool and bait will artificially attract predators into the traps (baited traps caught a higher number of predatory beetles than unbaited traps, see Chapter 3). It is therefore likely that baited traps in larger pools are actually sampling a larger area than traps in small pools (assuming the area of attraction in a large pool is larger than the area of a small pool), and also a larger area than unbaited traps, and therefore a higher number of individuals. Additionally, even assuming beetle density is similar in all pools, baited traps in large pools are likely to have a higher encounter rate (and therefore catch) than in small pools due to an increase in the total number of highly mobile individuals in the larger pools. Encounter rate will also be higher than for unbaited

traps because of the attraction of the bait. Baited traps between pools are identical and therefore the best explanation for lower catches in small pools is that there are fewer individuals in these pools to catch. A small pool may support a relatively low number of beetle individuals because of the finite biomass of potential prey items available and simple energetic constraints. Small populations are more prone to extinction (MacArthur & Wilson, 1963; 1967; Hanski, 1986), which leads to a reduction in species diversity on small islands where populations are small. The rescue effect would not seem to be effective amongst the predatory beetle taxa of these pools.

In predatory taxa, the rescue effect may be offset by the energetic requirements of an individual. Predators cannot be present without the required biomass of prey. In a small pool, despite immigration, energetic constraints may lead to few beetle larvae surviving, or adults may simply fly to another pool, thereby reducing the number of taxa. It is possible that the small pools in this study are large enough to support enough non-predatory individuals that, supplemented by the rescue effect, many non-predatory taxa are present and no relationship between pool area and number of non-predatory taxa is detectable.

It is probable that a pool-size threshold exists, below which the number of prey taxa in a pool will begin to reduce, as a consequence of a decrease in the number of individuals; such populations will be so small that the rescue effect cannot prevent extinction from that pool. This could be important for conservation and habitat fragmentation issues. However, it appears that the pools in this study were all above this threshold. There may also be a threshold in trophic rank, above which the rescue effect has limited influence on supplementing populations in small pools

because of the high energetic requirements of the individual. The model presented by Holt *et al*. (1992) predicts that species-area relationships should be stronger at higher trophic levels (when most consumers are specialists). This model is based on the conditional probability of a species being present, given that its required food source is present. They give several examples of data sets which show, some more convincingly than others, that species of a higher trophic rank have stronger species area relationships. It follows that weaker species-area relationships in the lower trophic levels are more likely to be masked by stronger influences, such as the rescue effect. In this system, predatory groups other than the diving beetles were either too rare (e.g. the Odonata) or too species poor (e.g. predatory Chironomidae) to test this theory. When all predatory taxa are considered, baited traps combined over all sampling months show a positive relationship with pool size. However, most of the predatory taxa are diving beetles which strongly determine this relationship.

Most of the taxa collected in the unbaited traps in April were microcrustacea, most of which are herbivores. Therefore the increase in number of all taxa with pool size in April is a consequence of the number of microcrustacean taxa present in the samples (compare Figure 4.2, Figure 4.3 and Figure 4.4). When all sampling periods are combined there is no effect of pool area. Additionally, two low taxon-counts in April appear to influence heavily the fit of the regression slope (Figure 4.3). However, movement of microcrustacea between pools may increase after April due to increased avifaunal activity during the breeding season. During the autumn and winter, decreased bird activity may result in the pools becoming isolated islands for the microcrustacea. A relationship may then start to establish between taxon density and pool area due to the extinction of small populations, which then breaks down in

the summer when increased avifaunal activity provides a rescue effect. The positive relationship with area for herbivore taxa (all microcrustacea) collected in the June baited traps has a low R^2 and may be a Type 1 error.

4.4.3 Sample-effort curves

Species accumulation curves showed that fewer taxa were collected in eight samples than were collected in twenty samples. This confirms that total species richness cannot be calculated from a small number of samples. These curves show that pool area does not determine either a) the rate of accumulation of taxa or b) the relative number of taxa collected at any point along the sample-effort curve in relation to other pools. Because the curves remain in a similar height order with an increase in the number of samples taken, reasonably accurate predictions of the relative orders of taxon richness can be made from the number of taxa in eight samples, for these data. For example, if Pool A has more taxa than Pool B at 8 samples, then Pool A is likely to have more taxa than Pool B at 20 samples.

Accordingly, testing the effect of pool size on species density using 8 samples per pool (from combining samples across all seasons) is likely to produce similar conclusions from using twenty samples per pool. These data may not be suitable for predicting accurate taxon richness, as this would involve large extrapolations from the smaller pools. However, an important feature of these plots is that the height of each curve is not related to pool size at any point along the x-axis. This, therefore, reinforces the conclusion that pool size has no effect on the number of taxa caught in a standardised number of samples and that there is no pattern in taxon richness along the pool size gradient.

4.4.4 Conclusions

Although many of the results were non-significant, there is a some weak evidence of a relationship between taxon density and area, shown by the general trend in Table 4.1. There are many positive slopes that approach significance and few negative slopes. However, this is only limited evidence of an increase in taxon density with area which suggests that size alone is not enough to create a species-area relationship, in most taxa.

The total species pool is relatively impoverished and, due to a strong rescue effect, is likely to be the main determinant of the number of taxa in a pool. Pool area may have a weak effect which appears to be taxon-specific, and possibly seasonal too. Area effects may be stronger if there were a larger species pool or if the smallest pools were smaller (without the confounding factors discussed earlier). The close proximity of the pools within the complex is an important factor in allowing assemblages to converge via the rescue effect.

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5 Factors influencing Community Structure

5.1 INTRODUCTION

The previous chapter showed that taxon density was generally not affected by pool area with the exception of the dytiscid diving beetles, which showed an increase in species density with pool area in the baited traps. This suggests that there may be more diving beetle species in the larger pools and that all other taxa appear to be unaffected by pool size. Counting the number of taxa, however, is not necessarily a good indicator of a community change over a gradient. Species richness has been shown to be less sensitive to environmental variation than community composition (Summerville & Crist, 2003) and may not be a good indicator, when considered alone, of community response to environmental influences. In this system, species turnover or variation in community composition and structure may occur over the pool size gradient without affecting taxon density.

This chapter considers the pool communities in three different ways. Firstly, abundance-occupancy relationships are plotted using the study pools and the possible mechanisms involved in creating such relationships are discussed. Secondly ratios of the numbers of predator:prey species are calculated for each pool and considered with respect to both pool area and total number of taxa per pool. Thirdly multivariate techniques are used to investigate community composition in each pool with respect to a number of environmental variables encompassing pool size, location and water chemistry.

5.1.1 Abundance-occupancy relationships

A positive relationship between the mean abundance of a species (over habitat-patches or sites occupied) and occupancy (number of habitat-patches or sites at which a species occurs) or range size has been well documented in the literature (e.g. Hanski, 1982; Brown, 1984; Gaston & Lawton, 1990; Maurer, 1990; Hanski, Kouki & Halka, 1993; Gaston, 1996; Venier & Fahrig, 1996; Warren & Gaston, 1997; Elmberg *et al.*, 2000). Studies show that abundant species tend to be widespread, occupying many sites, and species with low abundance tend to be more restricted in their distribution, occupying few sites. Although the relationship between the log of average abundance and occupancy has been represented as approximately linear (Hanski, 1982), low-abundance species seem to vary in their range of occupancy and so the relationship is often triangular in form (Warren & Gaston, 1997).

Many theories have been proposed to account for the positive relationship, often based on niche breadth (Brown, 1984), the importance of metapopulation dynamics (see review in Gaston, Blackburn & Lawton, 1997) and local abundance (Warren & Gaston, 1997; Gaston, 1999). The carrying capacity hypothesis (Nee, Gregory & May, 1991) predicts that high-abundance species have lower extinction rates and/or increased colonisation rates and hence occupy more patches at equilibrium, resulting in a positive abundance-occupancy curve. The rescue effect (Brown & Kodric-Brown, 1977) was suggested by Hanski (1991a; 1991b) to generate a positive relationship when immigration per patch increases as a function of occupancy and assumes that distribution affects abundance and vice versa. The rescue effect was implicated in causing abundance-occupancy relationships

(Gonzalez *et al.*, 1998) when experimental patches were connected by habitat corridors although Warren and Gaston (1997) found no effect of dispersal on the relationship in experimental microcosms.

Some studies have demonstrated that factors such as body size (Elmberg *et al.*, 2000) and disturbance (Gaston & Warren, 1997) also have no effect on patterns of local abundance (although see Holt, Warren & Gaston, 2002 where large bodied species did not maintain high occupancy). In a study of Australian marsupials (Johnson, 1998), range size and local abundance were found to be positively correlated for 'recently evolved' species and negatively correlated for 'ancient' species, indicating that positive relationships may be generated during adaptive radiation but are then gradually reversed. More recently, interspecific interactions in artificial aquatic communities were shown to reduce abundance per patch of many species thereby increasing the probability of species extinction and reduced occupancy (Holt *et al.*, 2002). Better-defined positive relationships were found in interacting communities than were found in non-interacting communities. In the natural habitat-patch system at Forsinard, although it was not possible to isolate the mechanisms that may be responsible for creating an abundance-occupancy relationship, the extent and shape of the curve may be observed and the potential processes involved discussed.

5.1.2 Predator:prey ratios

Broadly constant ratios of the number of predator taxa to the number of prey species have been suggested as a general characteristic of community and food web data (Cohen, 1977; Briand & Cohen, 1984; Pimm, Lawton & Cohen, 1991; Warren

& Gaston, 1992; Hall & Raffaelli, 1993) and many empirical studies support this (e.g. Arnold, 1972; Moran & Southwood, 1982; Jeffries & Lawton, 1985; Krüger & McGavin, 2001). Not all studies support the theory, however. Increases in the proportion of predator species have been reported across continuous gradients such as those of aquatic habitat patch-size (Spencer *et al.*, 1999), species number (Warren, 1989; Spencer *et al.*, 1999) and habitat permanence (Spencer *et al.*, 1999; Bilton, Foggo & Rundle, 2001). Differences in predator:prey ratios have also been reported between categorical variables such as habitat type (Hövemeyer, 1999). Some studies have simply refuted the 'constant ratio' theory as artefact (Closs, Watterson & Donelly, 1993) or myth (Wilson, 1996). In a study of several data sets, Warren and Gaston (1992) concluded that predator richness increased slightly faster than prey richness with an increase in species number, apparently due to a tendency for smaller communities to have few predator species but that predator and prey proportions were roughly scale invariant in larger systems.

In this study, the pattern in predator:prey ratios across a habitat patch-size gradient is investigated and the possible mechanisms involved are discussed. Ratios are considered with respect to pool area and number of species. Individual predator:prey ratios are considered for each of the study pools and a single ratio for the set of study pools as a whole is then calculated. An assumption is made that the set of study pools is representative of the complex as a whole. If the individual pool assemblages are a random sample of the whole complex then predator:prey ratios in each pool might be expected to be similar a) across the pool size gradient and b) to the ratio of the whole set of study pools. Alternatively, if each pool assemblage is structured individually in response to the size gradient and pools are responding as

separate communities within a meta-community of the whole complex, then individual predator:prey ratios might be expected to differ from that of the whole complex, or show a pattern across the size gradient.

Comparisons of ratios across systems, particularly between different studies, have historically suffered from problems arising from poor and inconsistent taxonomic resolution (Hall & Raffaelli, 1993; Thompson & Townsend, 2000) or inconsistent definition of predators and prey (Warren & Gaston, 1992). These problems are avoided in this study because taxa in all pools are identified to the same resolution and predators and prey categorised by a consistent definition. A reliable comparison of predator:prey ratios across the size gradient can therefore be made.

5.1.3 Community composition (multivariate techniques)

Taxon density is more-or-less independent of pool size in this system (see Chapter 4) but involves purely the number of taxa found and does not detect other possible variations in composition. In theory at least, species composition may vary over a range of pool sizes (or any other gradient) even if similar taxon density is maintained. A species, or taxon, may be present in several habitat patches but have its optimal distribution at a certain point along a particular gradient e.g. some measure of pool size. The effect of several species each with their distinctly different optima along a gradient would result in a shift in composition along that gradient. Species may also be completely replaced along a gradient, which measuring taxon density will not detect.

There is some evidence of community composition being more sensitive to environmental variables than species richness in butterfly communities (Summerville

& Crist, 2003). Alternatively, changes in species area relationships do not necessarily indicate changes in community structure (Ulrich & Buszko, 2003). Many studies of the effects of area concern themselves with counting the number of species or measuring population density and relatively few have used ordination techniques to identify changes in species composition. However, some studies carried out have shown contrasting results. Terrestrial beetle community structure was not affected by area in a recent study of Scottish woodlands (Woodcock, Leather & Watt, 2003) or in temporary wetlands in Germany (Brose, 2003). Studies of aquatic beetle communities however have shown changes in composition which can be, at least partly, attributed to some measure of habitat patch (pool) size (Fairchild, Faulds & Matta, 2000; Spencer, Schwartz & Blaustein, 2002; Rundle *et al.*, 2002).

Pool area was the only variable tested in Chapter 4 for an effect on taxon density, but area is not the only measure of pool size. Although they will obviously be highly correlated with area, an increase in perimeter or depth may be more important in terms of habitat availability. Despite all pools being close (within approx. 0.25 km^2) and dispersal constraints minimal, location within the pool complex may affect colonisation rates. The slight differences in water chemistry (which do not correlate with pool area) may also potentially influence community composition. Using multivariate techniques to analyse the variations in community composition is an appropriate way of determining both the maximum variation between communities and the variation that can be explained by measured environmental variables. The analysis is used to look at the data in different ways. Maximum turnover of taxa between pools is determined and correlated with the environmental gradients. Dissimilarities in pool composition are measured along

environmental gradients encompassing measures of size, location within the pool complex and water chemistry. Species' optima are calculated to determine which, if any, taxa are responding to which gradients.

5.2 METHODS

Data used in these analyses were the same as the data used in Chapter 4. Three sampling methods were used: baited and unbaited activity traps and sediment samples. More samples were originally taken from larger pools leading to a potential bias in the data due to an increased number of individuals being collected in the larger pools and the associated probability of increased diversity. As explained in detail in the previous chapter, this was corrected for by using an equal number of samples for each pool in analyses where the sampling bias was important. Analyses were repeated, where appropriate, using randomly selected samples from the larger pools, in order to use all data available. Taxa were included in the analyses at the lowest identification level possible. Unlike in the previous chapter, beetle larvae were categorised as separate taxa to the adults (as "*Genus* larvae") (except when calculating the predator:prey ratios) because of the different functions the larvae can have within a community compared to the adults. For example, larvae of *Dytiscus* are known to be important predators of tadpoles whilst the adults tend to take a wide range of invertebrate prey (Nilsson, 1996).

5.2.1 Abundance-occupancy relationships

Abundance-occupancy relationships were calculated for all taxa for each of the three sampling methods. Due to more samples being taken from the larger pools

for unbaited activity traps and sediment samples, the first three random selections of samples (from the ten random selections of samples used in Chapter 4) were used for each method. Similar results were found amongst the data sets within each sampling method and it was not felt necessary to carry out the calculations on all ten random selections of data for both methods.

Abundance was calculated by taking the mean density of a species across all pools in which it occurred. Occupancy was taken as the number of pools in which a species was recorded. Although occupancy could be calculated using all three sampling methods (adjusting for the bias in the sample number), calculating abundance would be more problematic because of the different taxonomic resolution between activity traps and sediment samples (i.e. chironomids were identified to family in sediment samples and genus in activity traps; microcrustacea were not recorded in the sediment samples) and the different biases of the sampling methods themselves. Therefore, the three sampling methods were considered independently. Data were pooled over the four sampling months; therefore the abundance of a particular patch (pool) was composed of four months' data. For certain pools, four months' data were not available and these pools were excluded from these analyses, hence the maximum occupancy shown in the results was < 22.

Although precise measurements of body-size were not available, it was possible to make comparisons based on extremes of body size observable by eye. For example the diving beetles and microcrustacea displayed obvious body-size differences and observations could be made from the data.

Spearman's rank correlation was carried out on each data set, which is appropriate for this type of non-linear data (Zar, 1999).

5.2.2 Predator:prey ratios

Predator:prey ratios were calculated for each pool. Prey taxa were defined as those that are non-predatory (categorised as herbivores and 'other' in Chapter 4). This is the same definition as used by Jeffries and Lawton (1985) where prey are all non-carnivorous taxa. Despite more samples being collected from larger pools, all samples from each pool were included in the analyses because ratios rather than absolute numbers were calculated, which would not be affected by an unbalanced sampling design. Predator:prey ratios for each pool were firstly calculated for each of the three different sampling methods and then by combining all sampling methods and using the combined list of taxa. Ratios were then regressed against pool area.

Ratio data were regressed on pool area using ordinary least squares regression. Ratio data were approximately normally distributed and therefore needed no transformation. Pool area data were log transformed to reduce the weighting of the largest pools. All regression analyses were carried out using Minitab for Windows software, version 12.

5.2.3 Community composition

To investigate patterns in community composition across the pool size gradient, and to investigate community response to other environmental gradients, multivariate techniques were used. Both indirect (unconstrained) and direct (constrained) gradient analysis was used for this purpose to look for a) the greatest axes of variability within the data set and b) the greatest axes of variability within the data that can be explained by the environmental variables. Data were analysed separately according to the three different sampling methods used for data collection

described in Chapter 3: baited and unbaited activity traps and sediment samples. In Chapter 4, ten balanced sets of randomly selected data were extracted from the unbaited activity traps and the sediment samples. Due to the extent of the multivariate analyses carried out on each data set, it was not practicable to carry out ordinations on all of the ten random sets of samples. The first three random selections of data for each of the above trapping methods were therefore used.

An increase in species richness with an increase in pool area had been detected in the baited activity traps due to an increase in the number of beetle species, presented in Chapter 4. Accordingly, all taxa and then, separately, the beetle taxa were analysed for patterns in community composition across the pool size gradient. In total, four categories of data were analysed, with two of the categories having three sets of randomly selected data (Table 5.1).

Table 5.1. Details of trap types and taxonomic groups used in multivariate analyses.

Trap Type	Taxa used in analysis
Baited Activity	All taxa
Baited Activity	Beetle taxa only
Unbaited Activity	All taxa (3 random sets of samples)
Sediment samples	All taxa (3 random sets of samples)

Because seasonal effects are not of interest in these particular analyses, (it is to be expected that composition will change to some degree due to the time of year the samples are collected) season was partialled out of (eliminated from) the analyses as a covariable. Therefore, in all the ordinations applied, gradients were fitted to the remaining variation in the data after the variation due to season had been subtracted. This is known as partial ordination. All ordinations were carried out using software for Canonical Community Ordination (CANOCO) version 4.5 (Ter Braak & Smilauer, 2002) and plotted using CanoDraw version 4.5.

Detrended Correspondence Analysis (DCA) (detrending by segments without transformation or down-weighting of rare species) was initially carried out on each data set to investigate gradient length and dissimilarity between samples. This type of ordination is unconstrained by any environmental variable and the gradients represent the 'optimal' predictors of the species responses, where sample scores are derived from the species data only. Environmental variables can be superimposed onto the results of the DCA without influencing the analysis and were projected onto the ordination diagram of sample scores. Thus, the level of correlation between environmental variables and ordination axes can be observed. Nine environmental variables were used: area, perimeter (Perim), maximum depth (Dmax), median depth (Dmed), Northing, Easting, distance of a) pool edge (PerifE) and b) pool centre (PerifC) from the centre of the complex, and pH.

The gradient length (DCA axis length) measures the extent of species turnover in community composition along each independent gradient (DCA axis). A gradient length of <3 indicates the data approximate a linear distribution and are therefore suitable for ordination methods based on a linear model (Leps & Smilauer, 2003). Gradient lengths >4 indicate that samples display complete species turnover and are suitable for ordination methods based on a unimodal model. Gradient lengths of between 3 and 4 may be suitable for either method. All gradient lengths were short (<3) for all data sets indicating only minimal species turnover and that linear ordination methods should be used. However, the species data contains many zeros and unimodal methods may be more appropriate for analysing such data, despite a short gradient length (Ter Braak & Smilauer, 2002).

To investigate which environmental variables were important in explaining the variation in the data, Canonical Correspondence Analysis (CCA) was applied. This is a constrained, unimodal method that may also be suitable for linear data (Ter Braak & Smilauer, 2002) and first axis extracts only that variation in the species data that can be explained by the environmental variables provided.

CCA was firstly carried out (with season partialled out as a covariable) using all nine environmental variables. The significance of the first ordination axis and of all canonical axes (those constrained by the environmental variables) together were tested using the Global permutation test in the CANOCO software. A second CCA was then carried out using the forward selection option and Monte Carlo permutations to rank each environmental variable by its importance and significance in determining patterns in the species data. When CCAs fitting only significant environmental variables were applied, the sum of all canonical eigenvalues were reduced by between 24 and 74%. Due to collinearity, the forward selection will remove a variable that explains a significant amount of variability when another, highly correlated, variable is selected first, as little extra variability remains to be explained by the second variable. Because the variables deemed as non-significant in the forward selection summary explain a substantial amount of the canonical variability (i.e. the amount of the above percentages), all environmental variables were kept in the model (although the highly non-significant variables could probably be removed with little effect). In order to look at species distributions with respect to each pool, pools were entered as categorical variables (numbers 1 - 22) in a third CCA and the centroids of samples according to category (pool number) were plotted

along with the species scores. Species are predicted to have their average relative frequency highest in the centroid (i.e. pool) closest to the species point.

The biplot scaling type was selected in the CANOCO software, for all CCAs, which is most suited for short gradients (ter Braak and Smilauer, 2002). Species scores were plotted, and so the scaling was focused on inter-species distances, which most accurately display the dissimilarities between the different species in the ordination diagram, although this does not affect the summary results of the analysis. (Inter-sample scaling is more appropriate when sample scores are plotted and distance between samples is of most importance).

5.3 RESULTS

5.3.1 Abundance-occupancy relationships

Because all the data sets come from the same pools, and not all taxa are included in every plot due to the different sampling method biases, it is advisable to consider all the plots when looking at the relationships. For all three sampling methods, a highly significant, positive relationship between mean abundance and occupancy was found (Figure 5.1, Table 5.2) which tended towards a triangular relationship. Species with low to moderate occurrences had low to moderate abundance, (with one exception in the baited activity traps); ubiquitous species had low to very high abundance. Low abundance taxa had low to high occupancy. The most widespread and abundant species were the microcrustacea, the smallest body-sized taxonomic group, although microcrustacea varied in both their distribution and abundance. Large bodied taxa tended to have less than 50% occupancy and low abundance. This is discussed further in Section 5.4.

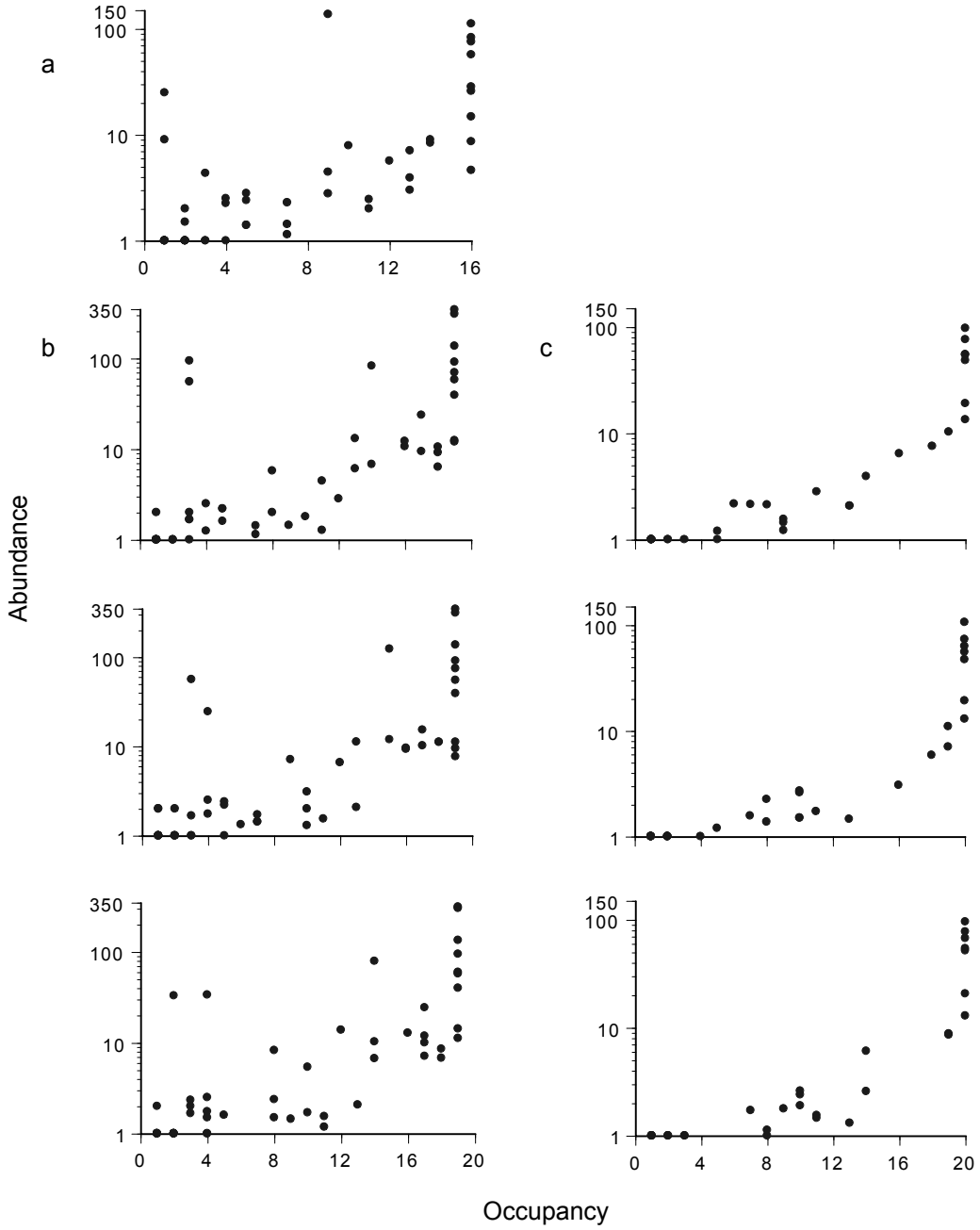

Figure 5.1. The relationship between the abundance (mean density per pool) and occupancy (number of pools occupied) for a) baited activity traps, b) three unbaited activity trap data sets and c) three sediment sample data sets. Abundance is shown on a log-scale. All relationships were significant, see Table 5.2.

Table 5.2. Results of Spearmans' rank correlation analysis for mean abundance and number of pools occupied for each of the three sampling methods. Correlation coefficient (r_s) and n are shown. All correlations were significant (P < 0.001).

	Data set 1		Data set 2		Data set 3	
	r_s	n	r_s	n	r_s	n
Baited activity traps	0.749	49	-	-	-	-
Unbaited activity traps	0.812	50	0.799	53	0.808	52
Sediment samples	0.951	33	0.955	33	0.938	31

5.3.2 Predator:prey ratios

Predator:prey ratios plotted against pool area for each of the three sampling methods and for all methods combined are shown in Figure 5.2. The mean proportion of predator species across all pools was 33%. The mean proportion of predators in the total species pool was only slightly higher at 35%. There was no significant relationship (P > 0.05) between predator:prey ratio and pool area for any individual sampling method or for all sampling methods combined (Table 5.3). No significant relationship was found (R^2 < 0.01; P > 0.05) between number of taxa and predator:prey ratios (all methods combined).

5.3.3 Community Composition

Summary results of ordinations carried out are presented, which detail how the variation in the data has been explained. The eigenvalue is a measure of the explanatory power of each of the axes (values between 0 and 1). The gradient length (DCA only) is measured in units of standard deviation (SD) and measures the amount of species turnover within the data (four standard deviations indicate complete species turnover amongst the samples). The total variability in the data, including that due to a covariable (season, in these analyses) is represented by Total

Inertia. After season has been partialled out the remaining variation is indicated by the sum of all eigenvalues. The sum of all canonical eigenvalues shows how much variation in the data can be explained by the environmental variables included in the analyses.

Table 5.3. Minimum, maximum and mean ± SD predator:prey ratios for three different sampling methods. Results of regression analyses against pool area (R^2 and P) are also presented. Degrees of freedom = 20.

Pool area (m^2)	Unbaited activity	Baited activity	Sediment samples	All methods combined
Minimum	0.29	0.21	0.25	0.34
Maximum	0.79	0.64	0.90	0.78
Mean	0.50 ± 0.13	0.41 ± 0.12	0.55 ± 0.16	0.49 ± 0.1
R^2	0.01	0.11	0.00	0.00
P	0.29	0.08	0.44	0.36

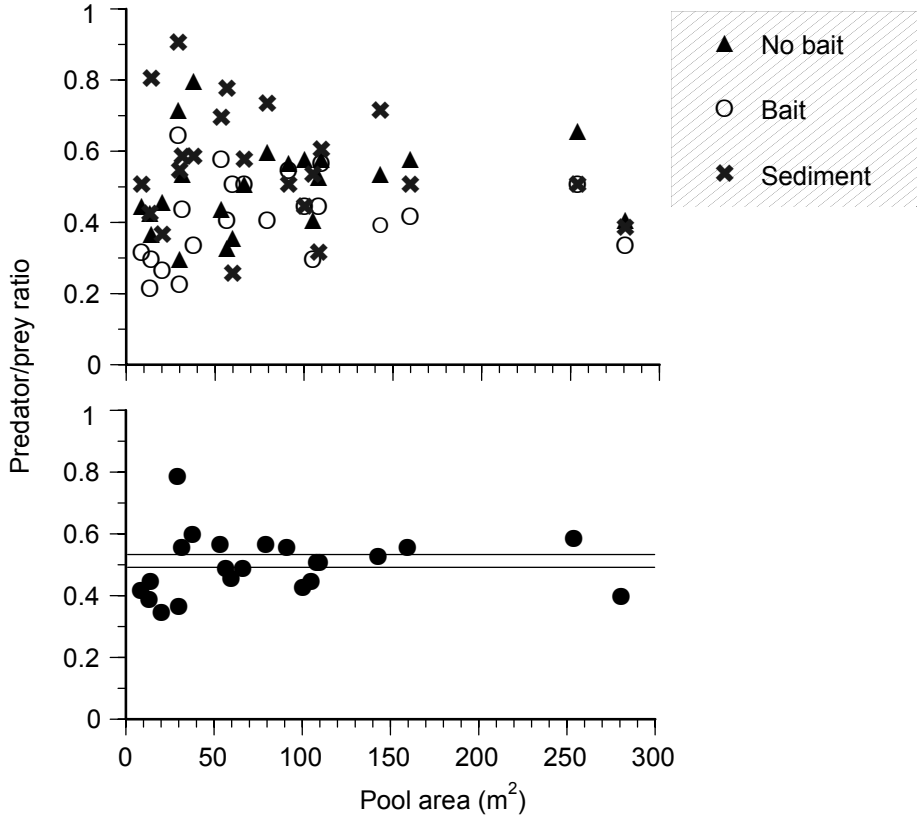

Figure 5.2 Predator:prey ratios per pool plotted against pool area for a) the individual sampling methods and b) all methods combined. Solid line represent the mean (± 0.1 SD) of the data points, dotted line represents the predator:prey ratio for the whole species pool.

a) Baited Activity Traps - All Taxa

Summary results of a partial DCA on the species data are presented in Table 5.4. Seasonal effects account for 15.9% of the variation in the data with the remaining variation due to other factors. The longest gradient is < 2 SD showing that there is little turnover between the samples. The first eigenvalue (which shows the amount of variation in the data explained by that axis) is close to twice the value of the second and explains 11.5% of the total species variability. The first axis correlates well with the environmental data (r = 0.717) while correlations for the other axes are much lower.

Sample scores of the 22 pools and the projected environmental variables are plotted in Figure 5.3. Samples are distributed in ordination space according to the dissimilarity of their species composition. The direction and length of the arrows representing the environmental variables show the direction and size of their correlation with species composition. The greater length, but lower eigenvalue, of the second axis is due to the outlying sample 8a. For illustrative purposes only, the samples have been divided into two size classes to highlight the dissimilarity between the smallest eleven and the largest eleven pools. Small and large pools show a relationship with the first axis with some overlap in the centre of the diagram. The environmental variables that are measures of pool size are closely correlated with the first axis, which although explaining only a small proportion of the total variation, explains the major axis of variation in the data. This suggests a small, but important, amount of community shift along the pool size gradient. Three measures of pool location (Northing, PerifE and PerifC) are correlated although any possible effect on species composition is confounded by a negative correlation with pool size.

Table 5.4. Summary results of partial DCA on baited activity trap data.

Axes	1	2	3	4	
Total inertia					1.235
Eigenvalues:	0.12	0.067	0.057	0.047	
Lengths of gradient:	1.588	1.835	1.493	1.014	
Species-environment correlations:	0.717	0.400	0.479	0.506	
Cumulative percentage variance of species data:	11.5	18.0	23.4	28.0	
Sum of all eigenvalues					1.039

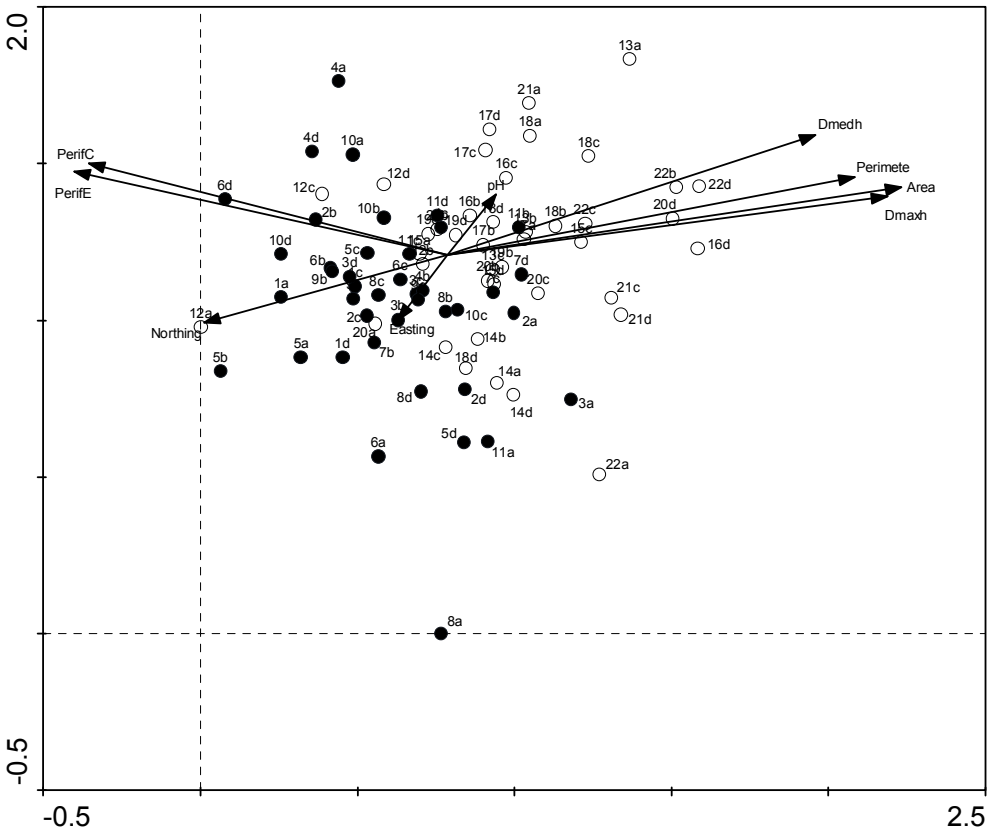

Figure 5.3. Sample scores and projected environmental variables of partial DCA, after removal of seasonal variation, on species data from baited activity traps. For illustrative purposes only, samples have been divided into two pool-size classes to highlight the dissimilarity of the eleven smallest (solid circles) and the eleven largest (open circles) pools in ordination space. Samples numbers relate to pool number (1 is the smallest and 22 the largest) and letters relate to the month of sampling (a = April, b = June, c = July, d = September).

Summary results of the CCA applied to the data can be seen in Table 5.5. As in the DCA, seasonal effects account for 15.9 % of the variation in the data. The

sum of all canonical eigenvalues (which shows the amount of variation in the data explained by environmental variables) accounts for 19.6 % of the remaining variation after the effect of season had been removed. The eigenvalue of each axis is much lower than in the DCA, due to the lower amount of variability that can be explained once the axes have been constrained to the environmental variables, the first explaining only 7.6 % of the variability after partialling out the effect of season. However, as would be expected from a constrained analysis, the first axis correlates well with the environmental variables (0.835) and explains 38.7 % of all canonical eigenvalues. The variation in the data remaining unexplained by season or environmental variables is 67.6 % of the total inertia.

Table 5.5. Summary results of partial CCA on baited activity trap data.

Axes	1	2	3	4	
Total inertia					1.235
Eigenvalues:	0.079	0.036	0.024	0.02	
Species-environment correlations:	0.835	0.83	0.686	0.679	
Cumulative percentage variance					
of species data:	7.6	11.1	13.3	15.2	
of species-environment relation:	38.7	56.3	67.8	77.5	
Sum of all eigenvalues					1.039
Sum of all canonical eigenvalues					0.204

The Global permutation tests revealed that the first canonical axis gave an F-ratio of 5.694 and was statistically significant ($P \leq 0.002$). The test of all canonical eigenvalues gave an F-ratio of 1.878 and a P-value of ≤ 0.002 showing that the relationship between the species and the environmental variables is significant. The amount of variation in the data explained by each variable is shown by 'Lambda' in the Forward Selection Summary in Table 5.6. Note that when all variables are considered independently, perimeter has a score of 0.05 (Lambda). When the Monte Carlo permutation tests are run with area added first to the model, perimeter no

longer adds a significant amount of extra fit, due to the high correlation between these two measures of pool size. In descending order of the F statistic, Area, PerifC, Dmax, PerifE and Dmed were all found to be significant in explaining variation in the data. Adding more variables did not significantly improve the fit.

Table 5.6. Forward Selection Summary and results of Monte Carlo permutation tests from CCA on baited species data. Lambda, (variability explained when each variable is tested independently), extra fit (variability explained in addition to that explained by previous variables), F-ratio and P-value of each environmental variable are shown. * variables significant at P ≤ 0.05; ** P < 0.01

Name	Lambda	Extra fit	F-ratio	P
Area	0.07	0.07	5.21	≤0.002**
PerifC	0.05	0.02	1.86	≤0.002**
Dmax	0.05	0.02	1.73	≤0.002**
PerifE	0.05	0.02	1.66	0.014*
Dmed	0.05	0.02	1.48	0.044*
Northing	0.03	0.02	1.39	0.07
Perim	0.05	0.01	1.37	0.074
Easting	0.02	0.02	1.12	0.26
pH	0.01	0.01	0.73	0.84

Species scores and environmental variables have been plotted on the first two axes in Figure 5.4. The distance between the species points approximates the chi-square distance between the species distributions. Perpendicular lines projected from the species points onto an environmental arrow give an approximate ordering of the "species' optima" (where a species is at it's most abundant). The taxon which projects a perpendicular line most distally along the arrow will have its optimum distribution at the highest (or lowest if projected onto the negative part of the gradient) value of that variable compared to other species. Area is the most important explanatory variable in this ordination and the taxa with their respective optima at the ten highest and the ten lowest points along this gradient are shown in Table 5.7.

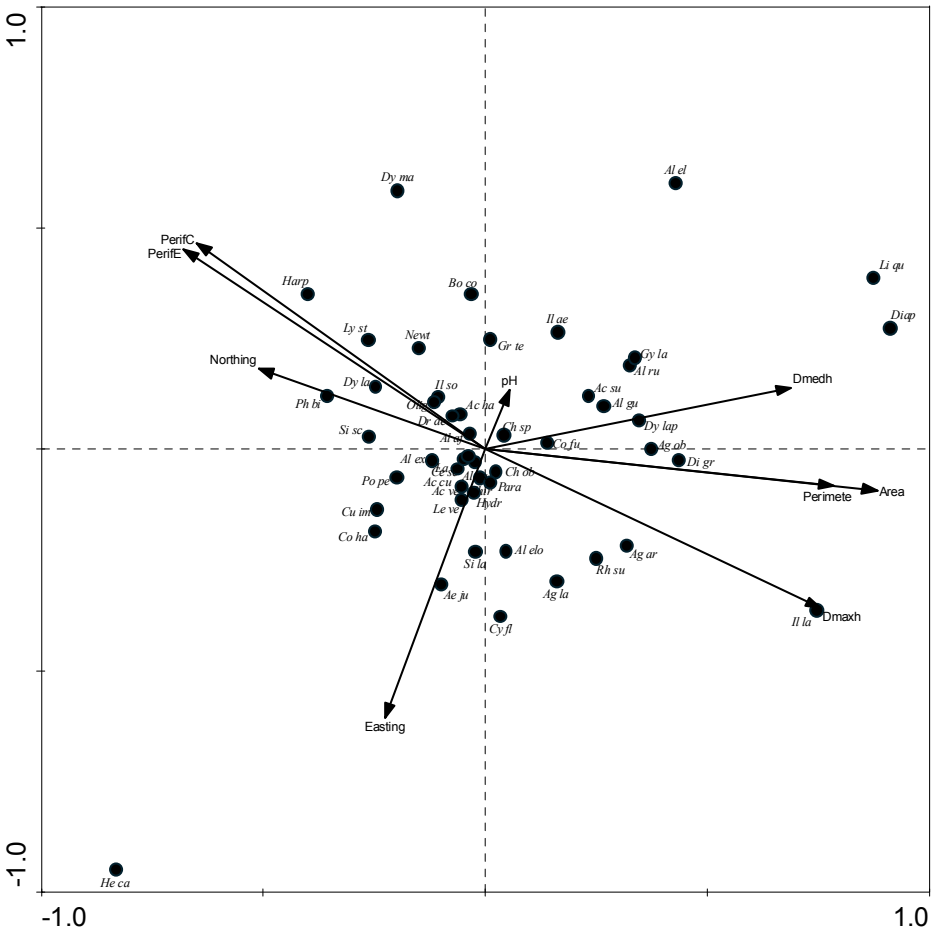

Figure 5.4. Species scores and environmental variables of partial CCA on species data from baited activity traps. Species codes are shown in Appendix 1.

Table 5.7. Taxa with optimal distributions at the ten highest and ten lowest points along the area gradient of CCA, in most distal order, for baited activity traps. Taxa in bold were also found at one of the ten lowest (if a low value taxa) or highest (if a high value taxa) positions along the area axis in unbaited activity traps. † denotes a diving beetle and ° a microcrustacean. High value taxa suffixed with * were also found at one of the ten lowest positions in the unbaited traps. Low value taxa suffixed with * were also found at one of the ten highest positions in unbaited traps.

High values	Low values
°***Diaphanosoma* sp.**	*Hesperocorixa castanea*
*Libellula quadrimaculata**	°**Harpacticoida**
†*Ilybius* larvae*	***Phryganea bipunctata***
°***Diaptomus gracalis***	*Lymnephilus stigma*
*Agrypnia obseleta**	*Sigara scotti**
°***Alona elegans***	†*Dytiscus marginalis**
†***Dytiscus lapponicus***	†*Dytiscus* larvae*
†***Agabus arcticus***	*Culicoides impunctatus*
***Gyrinus* larvae**	***Coenagrion hastulatum***
°*Alona rustica*	°*Polyphemus pediculus*

By plotting the samples from each pool as a centroid (average score) together with the species scores (see Figure 5.5), the relative total abundance of a species (i.e. summed over all the samples relating to that centroid) can be seen with respect to each pool. The average relative abundance of a species is predicted to be highest in the samples of the centroid closest to the species point. The same species that are highest on the area axis in Figure 5.4 are situated close to large pools in Figure 5.5. Many species are located close to large pools whilst few species have their optimal distributions in small pools.

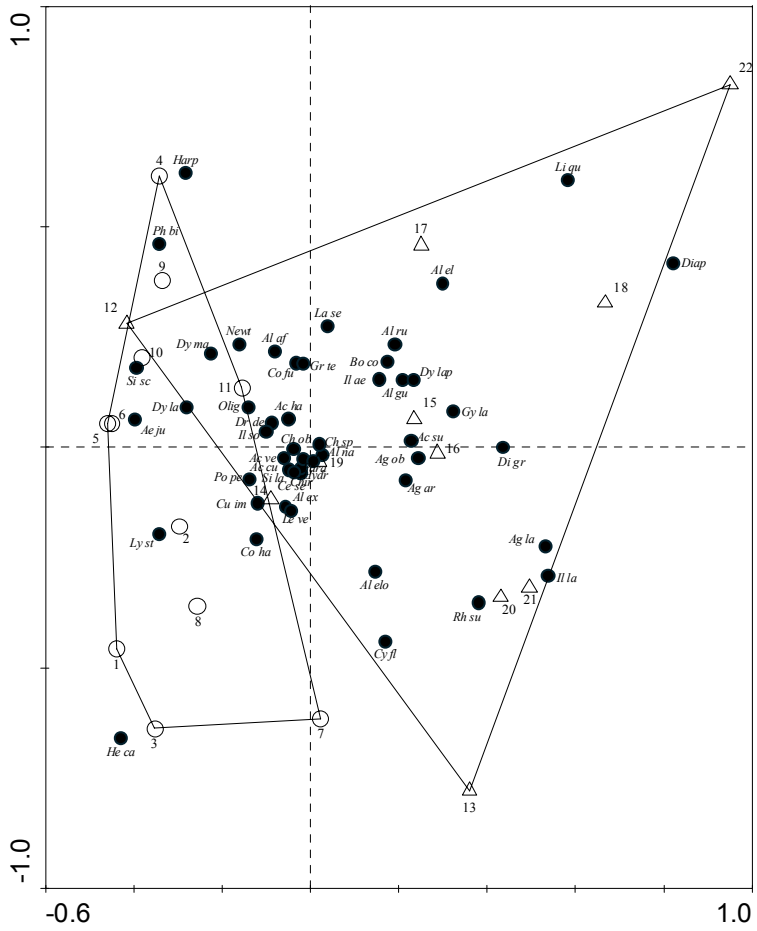

Figure 5.5. Centroids (pool number) and species scores for CCA on baited activity traps. The polygons are the smallest convex polygon that enclose the centroids for the eleven smallest (1 – 11, open circles) and the eleven largest (12 – 22, open triangles) pools. Species codes are shown in Appendix 1.

b) Baited Activity Traps - Beetle Taxa

Summary results of the partial DCA on the beetle data only are shown in Table 5.8. Seasonal effects account for 17.5 % of the variation in the data. The first gradient is > 4 SD indicating a complete turnover in beetle species composition amongst the samples and the eigenvalue indicates this axis explains 23.9 % of the variability. The second axis also explains a considerable amount of variation (17.9 %). The first axis shows the least correlation with the environmental data, the highest correlation being shown by the second axis.

Table 5.8. Summary results of partial DCA on beetle data from baited activity traps.

Axes	1	2	3	4	
Total inertia					3.223
Eigenvalues:	0.636	0.477	0.23	0.087	
Lengths of gradient:	4.598	2.678	2.701	2.406	
Species-environment correlations:	0.328	0.616	0.562	0.481	
Cumulative percentage variance of species data:	23.9	41.8	50.5	53.7	
Sum of all eigenvalues					2.660

The plot of sample scores and environmental variables in Figure 5.6 reveal that the gradient length of the first axis is due to a single sample (18c) showing a large dissimilarity from the other samples, apparently not attributable to any measured environmental variable. There is some community shift between small and large samples although this is less clear than in the plot of all taxa. The overlap of many of the samples caused by identical composition can be expected due to the low beetle abundances. Low beetle abundance will also increase noise in the data due to sampling error. The environmental variables that are measures of pool size are

closely correlated with the second axis, which explains most of the variation in the data if the outlying sample is ignored. This again suggests a small but important amount if community shift in the beetle data along the pool size gradient.

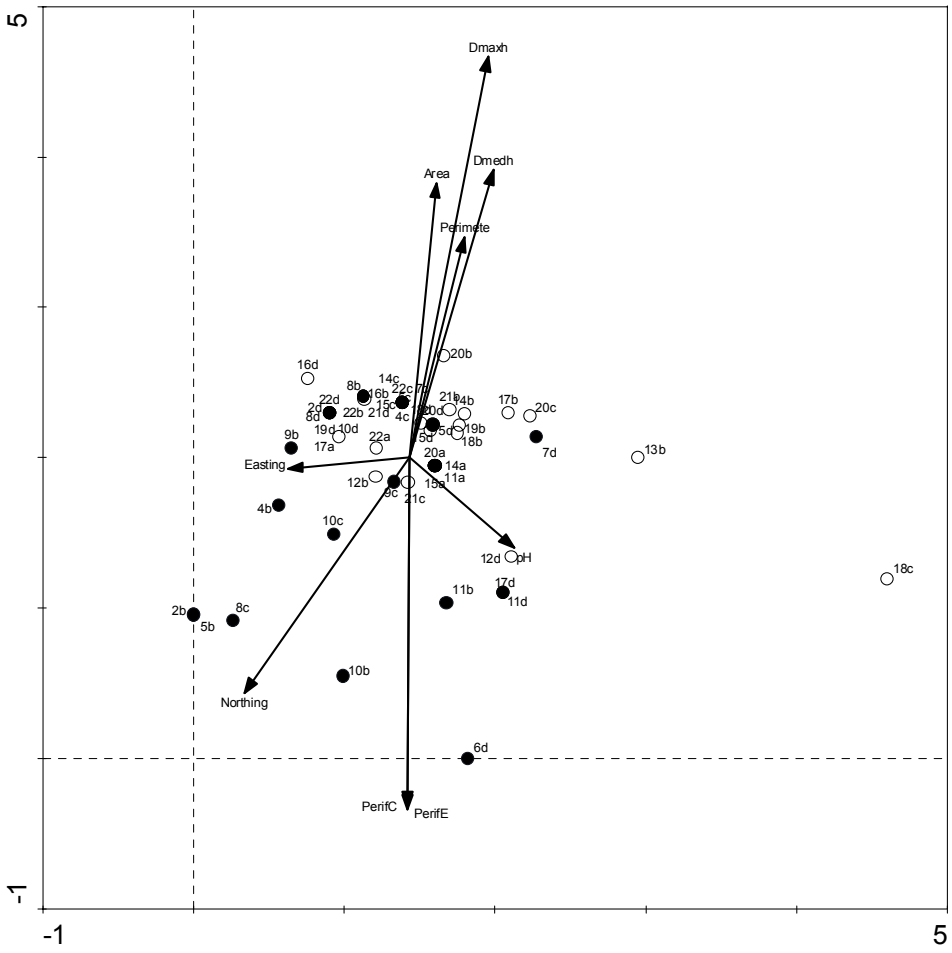

Figure 5.6. Sample scores and projected environmental variables of partial DCA on beetle data from baited activity traps. Samples from the smallest eleven pools are represented by closed circles and from the largest eleven pools by open circles. Although samples will not be present if they do not contain beetle taxa, many samples have similar composition and are located close together in ordination space.

Summary results of partial CCA applied to the data can be seen in Table 5.9. The sum of canonical eigenvalues explains 21.6 % of the remaining variability in the data after the effect of season had been removed. Again the eigenvalue of each axis is lower than in the DCA, explaining only 8.4 % of the variability. The first and second axes correlate equally with the environmental data although the first explains more of the variation (38.8 % compared to 21.6 %). The variation in the data remaining unexplained by season and environmental data is 64.7 % of the total inertia.

Table 5.9. Summary results of partial CCA on beetle data from baited activity traps.

Axes	1	2	3	4	
Total inertia					3.223
Eigenvalues:	0.223	0.124	0.092	0.061	
Species-environment correlations:	0.631	0.629	0.515	0.419	
Cumulative percentage variance					
of species data:	8.4	13	16.5	18.8	
of species-environment relation:	38.8	60.4	76.5	87	
Sum of all eigenvalues					2.660
Sum of all canonical eigenvalues					0.574

The global permutation tests revealed that neither the first nor all the canonical axes together were significant ($F = 3.474$, $P = 0.26$; $F = 1.162$, $P = 0.19$). Forward selection of each environmental variable was still carried out to test whether any single variable had a significant effect on the beetle species data. The forward selection summary (Table 5.10) shows that only maximum depth is significant at the 5 % significance level, explaining a relatively large amount of variability compared to the other variables.

Table 5.10. Summary of Forward Selection results of CCA on beetle data from baited activity traps. Extra fit explained by a variable after the addition of the previous variable to the model, F-ratio and P-value of each environmental variable are shown. * variables significant at P < 0.01.

Variable	Lambda	Extra fit	F-ratio	P
Dmax	0.18	0.18	3.31	0.004*
Northing	0.10	0.05	1.03	0.402
Easting	0.05	0.05	0.94	0.508
pH	0.03	0.04	0.71	0.664
Area	0.08	0.04	0.67	0.636
Perim	0.07	0.07	1.26	0.280
PerifC	0.12	0.04	0.74	0.624
PerifE	0.12	0.06	1.18	0.262
Dmed	0.10	0.04	0.75	0.606

In the biplot of species scores and environmental axes (Figure 5.7) *Ilybius* larvae*, Agabus arcticus, Agabus* larvae*, Colymbetes fuscus* and *Rhantus suturellus* have their optima at the highest values along this maximum depth gradient and *Dytiscus marginalis, Dytiscus* larvae, and *Ilybius aenescens* have their optima at the lowest values.

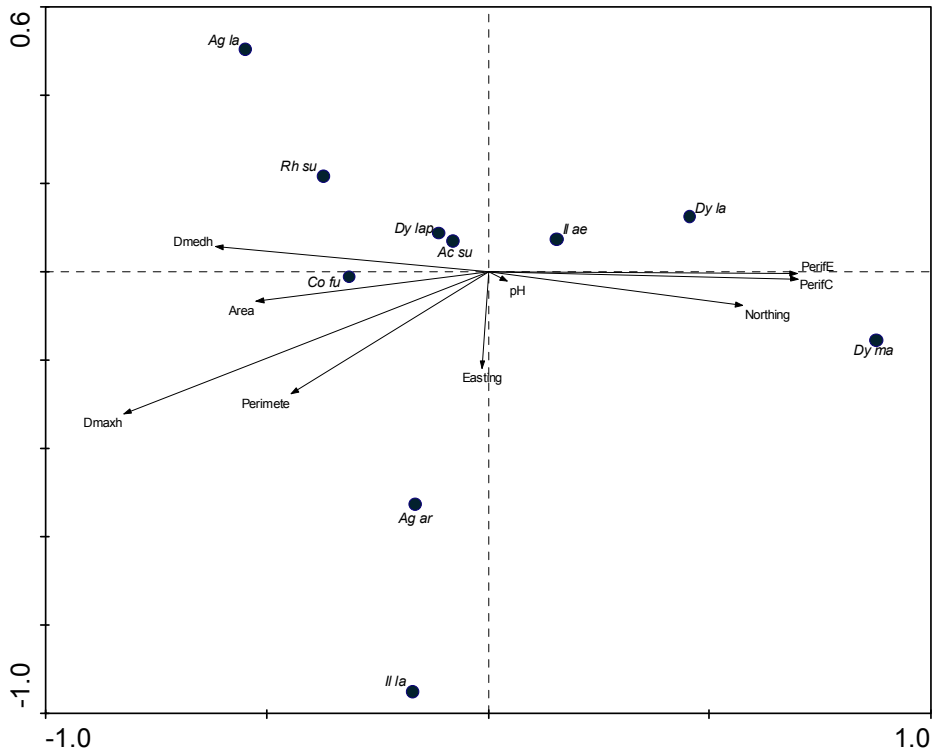

Figure 5.7. Species scores and environmental variables of partial CCA on beetle data from baited activity traps. Species codes are shown in Appendix 1.

c) Unbaited Activity Traps

Partial DCA was carried out on three sets of randomly selected data from unbaited activity traps. Gradient lengths were all <2 SD indicating very little turnover between the samples and that the data approximated a linear distribution. Total inertia ranged from 1.038 to 1.07 with seasonal effects explaining between 20.6 % and 21.8 % of the variation. The eigenvalues of the first axes represent between 11.6 % and 13 % of the variability in the data after removal of seasonal effects, which is approximately double that explained in the next highest axis in each ordination. The first axes correlate well with the environmental data (0.715 - 0.718) with other axes all < 0.6. The sums of all canonical eigenvalues range from 0.104 to 0.124, explaining between 18.4 and 19.4 % of remaining variability after partialling out season. Sample scores of all three analyses are plotted in Figure 5.8. The separation of the two size categories is along the first gradient, which explains the optimal variation in the data, showing again a small but important amount of community shift with an increase in pool size.

In the partial CCA applied to each data set, with axes constrained to the environmental variables, the eigenvalues were again much lower than in the DCA, the first axes explaining between 7.3 and 7.9 % of the variability after the effect of season was removed. The first axes correlate well with the environmental data (0.797 to 0.815) and explain between 39.5 and 40.8 % of all canonical eigenvalues. Variation in the data remaining unexplained is between 63.9 and 64.6 % of the total inertia. Global permutation tests revealed that the relationships between species and the environmental variables were significant at $P \leq 0.002$ for the first canonical axis and all canonical eigenvalues together, in all three data sets. Variability explained by

each environmental variable is shown is the Forward Selection summary in Table 5.11. For all three data sets, area explained the highest amount of the variation in the data compared to other variables.

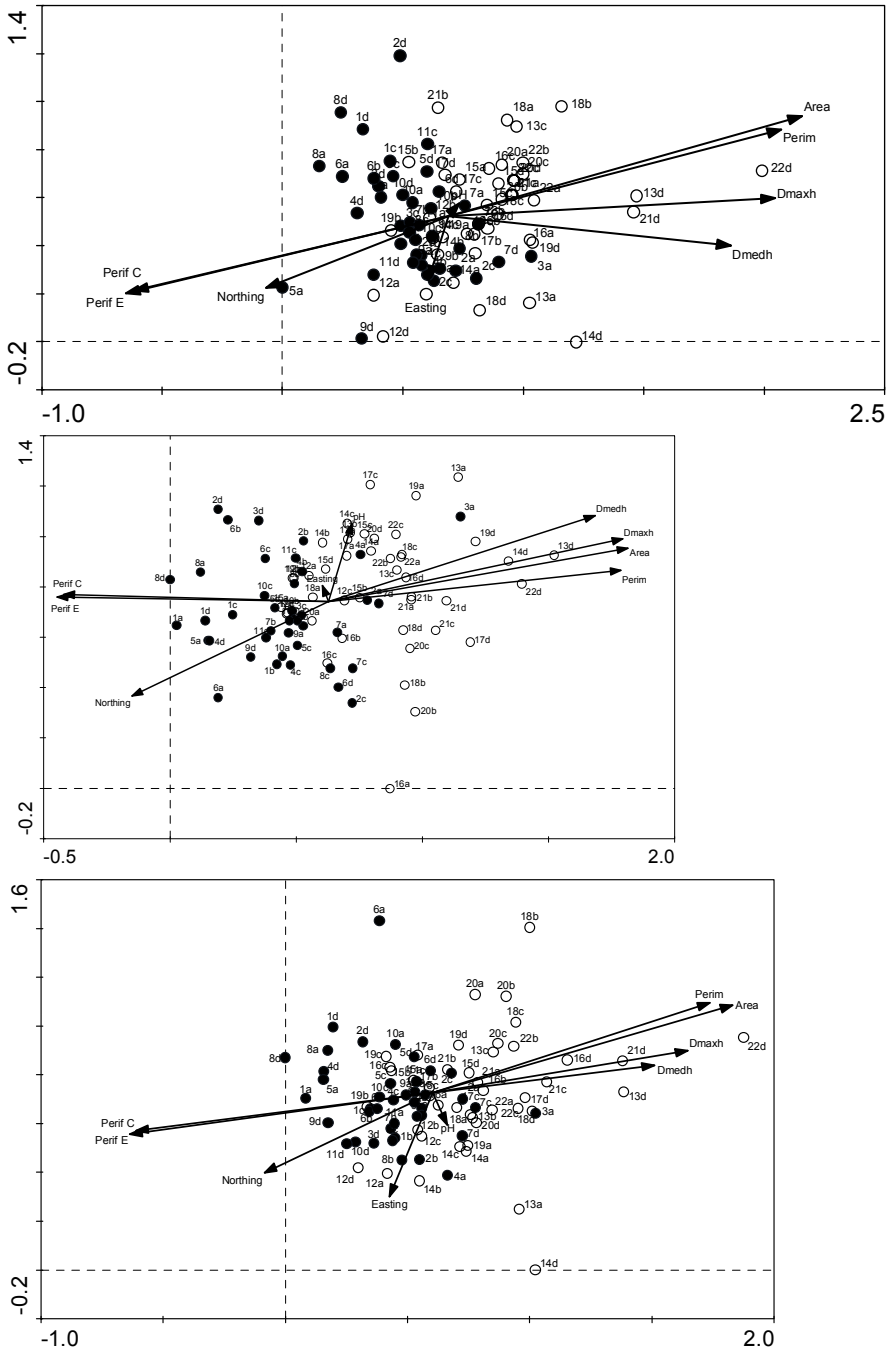

Figure 5.8. Sample scores and projected environmental variables of partial DCA on unbaited activity trap species data. a) data set 1, b) data set 2, c) data set 3. Samples from the smallest eleven pools are represented by closed circles and from the largest eleven pools by open circles.

Table 5.11. Forward selection summary and results of Monte Carlo permutation tests for each of the three random data sets from unbaited activity traps. Lambda (variability explained when each variable is tested independently), extra fit (variability explained in addition to that explained by previous variables), F-ratio and P-value of each environmental variable are shown. * variables significant at P ≤ 0.05.

Data set	Variable	Lambda	Extra fit	F	P
1)	Area	0.05	0.05	5.67	≤0.002*
	Dmed	0.04	0.03	2.33	≤0.002*
	PerifC	0.04	0.01	1.74	0.014*
	Northing	0.03	0.02	1.42	0.056
	Dmax	0.04	0.01	1.28	0.122
	Easting	0.01	0.01	1.23	0.196
	Perim	0.05	0.01	1.08	0.326
	pH	0.01	0.01	1.04	0.326
	PerifE	0.04	0.01	0.81	0.734
2)	Area	0.05	0.05	5.38	≤0.002*
	Dmed	0.04	0.03	2.22	≤0.002*
	PerifC	0.04	0.01	1.57	≤0.020*
	Perim	0.05	0.01	1.38	0.064
	Northing	0.03	0.02	1.24	0.194
	Easting	0.01	0.01	1.21	0.218
	Dmax	0.04	0.01	1.10	0.294
	PerifE	0.04	0.01	1.00	0.448
	pH	0.01	0.01	0.91	0.472
3)	Area	0.06	0.06	5.86	≤0.002*
	PerifC	0.05	0.02	2.14	≤0.002*
	Dmed	0.04	0.02	1.97	0.004*
	Northing	0.03	0.01	1.49	0.044*
	Dmax	0.04	0.01	1.40	0.064
	Easting	0.01	0.02	1.34	0.110
	pH	0.01	0.01	1.02	0.364
	Perim	0.05	0.00	0.81	0.738
	PerifE	0.05	0.01	1.01	0.452

Species scores and environmental variables plotted on the first two CCA axes for each data set can be seen in Figure 5.9. Area is the most explanatory variable in all three diagrams and taxa that have their respective optima at the ten highest or ten lowest values along this gradient, for each data set, are shown in Table 5.12.

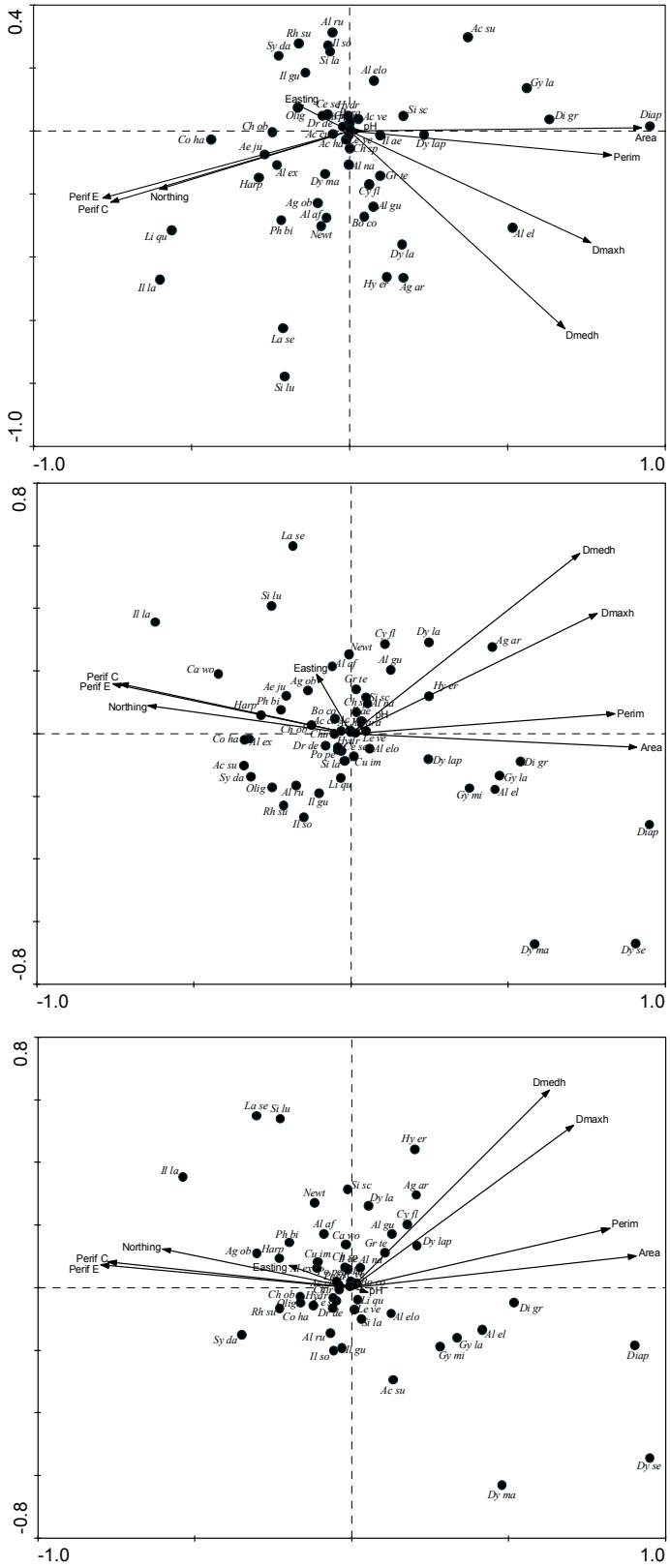

Figure 5.9. Species scores and environmental variables of partial CCA on species data from unbaited activity traps. a) Data set 1, b) data set 2, and c) data set 3. Species codes are shown in Appendix 1.

Table 5.12. Taxa with optimal distributions at the ten highest and the ten lowest points, in most distal order, along the area gradient, for each random selection of data. Taxa in bold were also found at one of the ten highest (if a high value taxa) or lowest (if a low value taxa) positions along the area axis in baited activity traps. High value taxa suffixed with * were also found at one of the ten lowest positions in the baited traps. Low value taxa suffixed with * were also found at one of the ten highest positions in the baited traps. † denotes a diving beetle and ° a microcrustacean.

Data 1	Data 2	Data 3
High values		
°***Diaphanosoma* sp.**	°***Diaphanosoma*** sp.	†*Dytiscus semisulcatus*
°***Diaptomus gracalis***	†*Dytiscus semisulcatus*	°***Diaphanosoma*** sp.
***Gyrinus* larvae**	†*Dytiscus marginalis**	°***Diaptomus gracalis***
°***Alona elegans***	°***Diaptomus gracalis***	†*Dytiscus marginalis**
†*Acilius sulcatus*	***Gyrinus* larvae**	°***Alona elegans***
†***Dytiscus lapponicus***	°***Alona elegans***	***Gyrinus* larvae**
†***Agabus arcticus***	†***Agabus arcticus***	*Gyrinus minutus*
†*Dytiscus* larvae*	*Gyrinus minutus*	†*Hydroporus erythrocephalus*
*Sigara scotti**	†***Dytiscus lapponicus***	†***Agabus arcticus***
†*Hydroporus erythrocephalus*	†*Hydroporus erythrocephalus*	†***Dytiscus lapponicus***
Lowest values		
†*Ilybius* larvae*	†*Ilybius* larvae*	†*Ilybius* larvae*
*Libellula quadrimaculata**	*Callicorixa wollastoni*	*Sympetrum danae*
Coenagrion hastulatum	***Coenagrion hastulatum***	*Agrypnia obseleta**
°**Harpacticoida**	†*Acilius sulcatus*	†*Rhantus suturellus*
Aeshna juncea	°*Alonella excisa*	°*Latona setifera*
Chaoborus obscuripes	*Sympetrum danae*	°**Harpacticoida**
°*Alonella excisa*	°**Harpacticoida**	***Phryganea bipunctata***
Phryganea bipunctata	*Sialis lutaria*	Oligochaetae
°*Latona setifera*	Oligochaetae	*Chaoborus obscuripes*
Sialis lutaria	***Phryganea bipunctata***	*Sialis lutaria*

d) Sediment Samples

Partial DCA was carried out on three sets of randomly selected data from sediment samples. The first gradients were 2.5, 2.7 and 3.2 standard deviations long respectively, indicating more turnover between samples than in the activity traps although still less than a complete turnover. However, in data sets 2 and 3, a single outlying sample considerably extended the length of the 1st gradient. Further investigation revealed this sample (the same sample had been chosen for that month in both data sets 2 and 3) contained a very low number of individuals and taxa compared to all other samples, including those from the same pool on different

sampling occasions. It was therefore deemed an atypical sample and removed from the analysis.

When DCA was used without the outlying sample in data sets 2 and 3, the first gradient lengths of all 3 data sets were 2.5, 1.6 and 1.9 respectively. Total inertia ranged from 1.023 to 1.171 with seasonal effects explaining between 26.1 and 27.9 % of the variation. The eigenvalues of the first axes explain between 12.9 and 15.2 % of the remaining variation in the data and the first and second together between 21.4 and 23.7 %. The first axes correlate less clearly with the environmental variables (max = 0.64) than the activity traps. Sample scores of the three data sets are plotted in Figure 5.10. There is some segregation of the two pool size classes, although this is less clear than in the activity traps, with a large amount of overlap around the centroid of sample scores. The segregation of the two pool size categories in each diagram shows some correlation with the first axis in data sets 2 and 3 and with the second axis in data set 1.

In partial CCA applied to the data sets the eigenvalues of the first axes were very low compared to those in DCA, explaining between only 4.3 and 6 % of the variability after the effect of season was removed. The first axes show some correlation with the environmental variables (0.60 to 0.70) and explain between 29.5 and 38.4 of all canonical eigenvalues. The sums of all canonical eigenvalues range from 0.100 to 0.123, explaining between 13.5 and 15.5 % of the remaining variability after season has been partialled out. Variation remaining unexplained by either season or the environmental variables was between 60.9 and 63.4 % of the total inertia. Despite low correlations between the axes and the environmental data, Global permutation tests revealed that the relationships between species and the

environmental variables, in all three data sets, were significant at $P < 0.03$ for the first axes and $P < 0.004$ for all canonical axes together. Variability explained by environmental variables is shown in the Forward Selection summary in Table 5.13. Either pool area or measures of pool depth were the only significant predictors of the species distributions.

Table 5.13. Forward selection summary and results of Monte Carlo permutation tests for each of the three sets of species data from sediment samples. Lambda (variability explained when each variable is tested independently), extra fit (variability explained in addition to that explained by previous variables), F-ratio and P-value of each environmental variable are shown. * variables significant at $P \leq 0.05$; ** $P < 0.01$.

Data set	Variable	Lambda	Extra fit	F	P
1)	Area	0.02	0.02	1.78	0.014*
	Dmax	0.02	0.02	2.04	0.004**
	Easting	0.01	0.01	1.33	0.102
	Perim	0.02	0.02	1.43	0.074
	PerifE	0.02	0.01	1.06	0.254
	PerifC	0.02	0.01	1.40	0.068
	Dmed	0.02	0.01	1.15	0.210
	Northing	0.01	0.01	1.01	0.330
	pH	0.01	0.01	0.82	0.450
2)	Area	0.02	0.02	2.12	0.004**
	Dmax	0.02	0.02	1.92	0.006**
	Easting	0.01	0.01	1.24	0.182
	Perim	0.02	0.01	1.18	0.214
	PerifE	0.01	0.01	1.08	0.264
	Dmed	0.02	0.01	0.98	0.444
	PerifC	0.01	0.01	1.02	0.334
	pH	0.01	0	0.88	0.432
	Northing	0.01	0.01	0.82	0.660
3)	Dmed	0.03	0.03	3.3	<0.002**
	Dmax	0.02	0.01	1.35	0.088
	Area	0.03	0.02	1.99	0.004**
	PerifC	0.01	0.01	1.27	0.150
	Easting	0.01	0.01	1.14	0.282
	Perim	0.03	0.01	1.02	0.330
	PerifE	0.01	0.01	1.16	0.192
	Northing	0.01	0.01	1.01	0.360
	pH	0.01	0.01	0.88	0.414

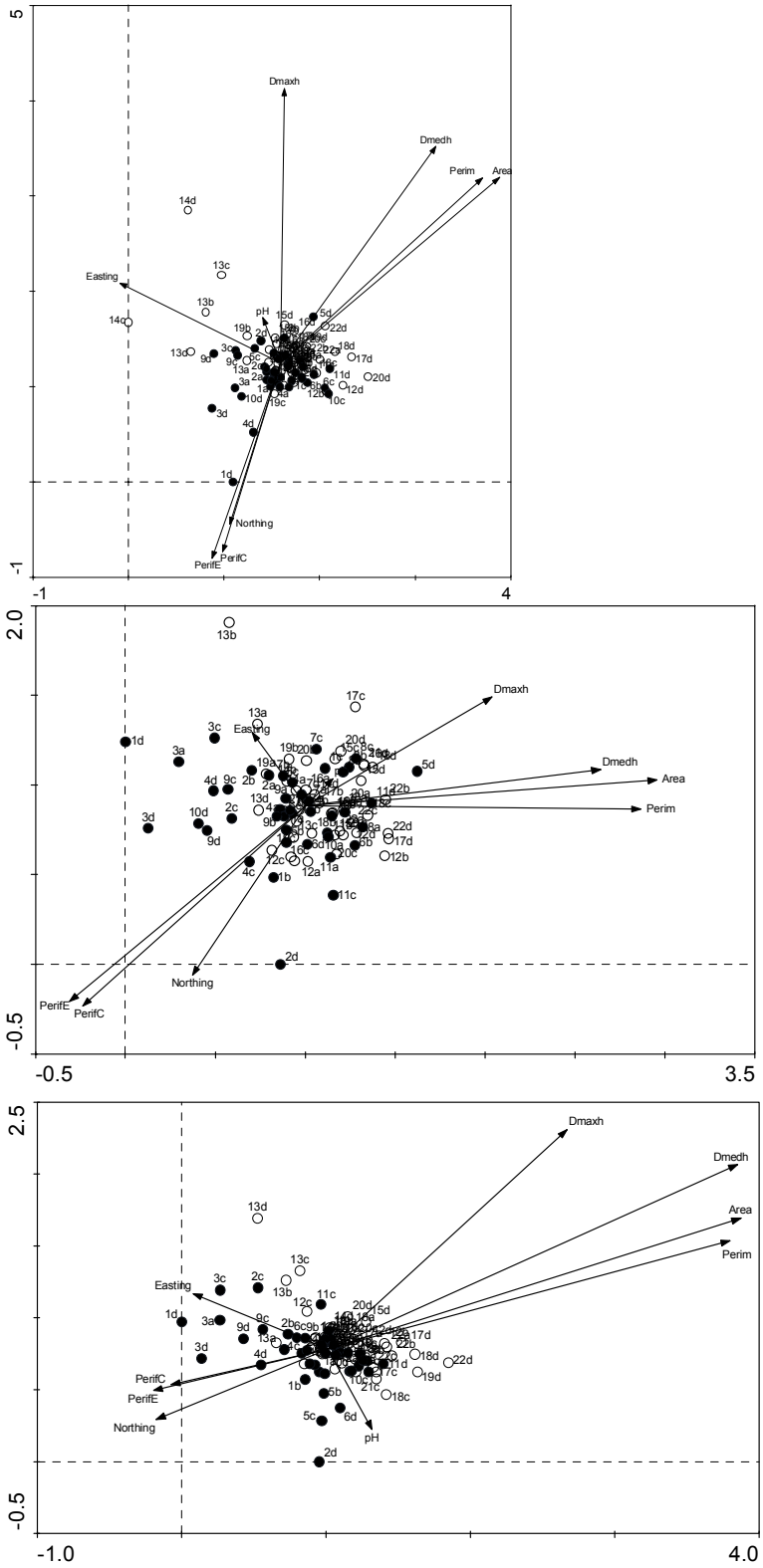

Figure 5.10. Sample scores and projected environmental variables of partial DCA, excluding outlier in b) and c), on sediment sample species data, a) data set 1, b) data set 2, and c) data set 3. For illustrative purposes only, samples have been divided into two pool-size classes to highlight dissimilarity between the eleven smallest (closed symbols) and the eleven largest (open symbols) pools in ordination space.

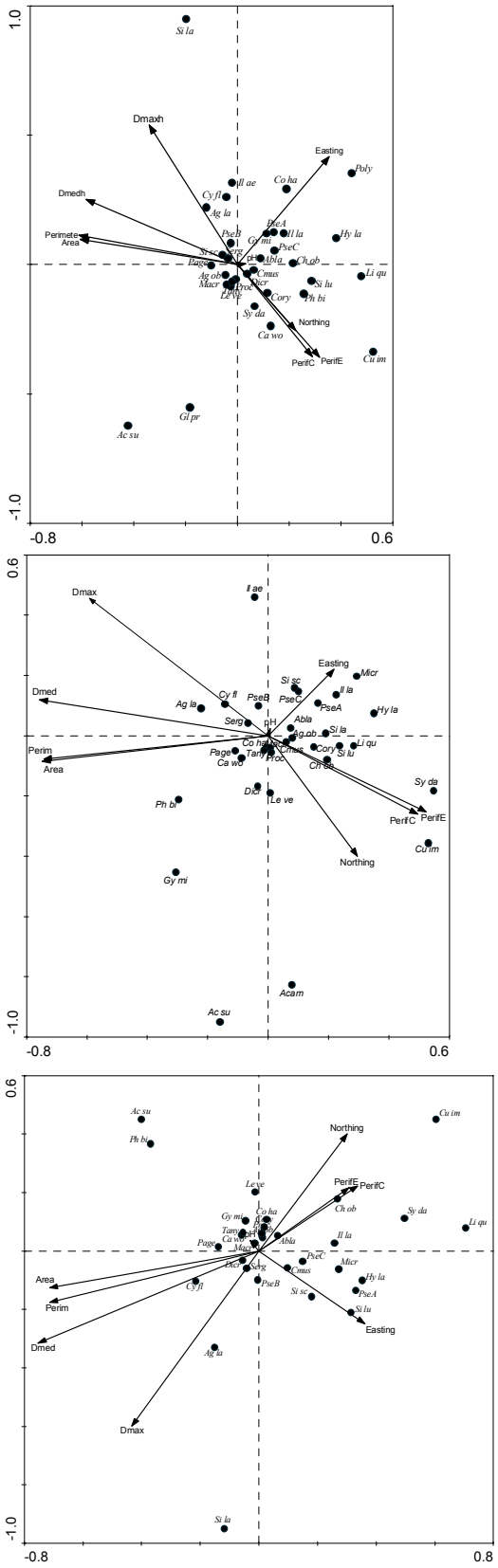

Figure 5.11. Species score and environmental variables of partial CCA on species data from sediment samples. a) Data set 1), b) data set 2, and c) data set 3. Species codes are shown in Appendix 2.

Species scores and environmental variables of each data set are plotted in Figure 5.11. The most explanatory variables in the CCA were maximum depth for data set 1, area for data set 2 and median depth for data set 3. Species that have their optima at the highest values along these gradients are shown in Table 5.14.

Table 5.14. Taxa with their optimal distributions at the four highest and four lowest points along the most significant gradients, in most distal order, for each random selection of sediment sample data. The most significant gradient in the CCA applied to each data set is shown in parenthesis. † denotes a diving beetle taxon.

Data 1 (maximum depth)	Data 2 (area)	Data 3 (median depth)
Highest values		
Sigara larvae	*Gyrinus minutus*	†*Agabus* larvae
†*Ilybius aenescens*	*Phryganea bipunctata*	*Cyrnus flavidus*
†*Agabus* larvae	†*Agabus* larvae	*Phryganea bipunctata*
Cyrnus flavidus	*Cyrnus flavidus*	†*Acilius sulcatus*
Lowest values		
Culicoides impunctatus	*Sympetrum danae*	*Culicoides impunctatus*
Glaenocorixa propinqua	*Culicoides impunctatus*	*Libellula quadrimaculata*
Libellula quadrimaculata	†*Hydroporus* larvae	*Sympetrum danae*
Callicorixa wollastoni	*Microtendipes* sp.	*Chaoborus obscuripes*

5.4 DISCUSSION

5.4.1 Abundance-Occupancy Relationships

Taxa show a distinct, positive abundance-occupancy relationship. The mechanisms causing this relationship cannot be tested using these data and results should be interpreted with care. There are few samples in each calculation of abundance (abundance per pool is calculated from eight activity traps for both baited and unbaited, and three sediment samples respectively). This means that only a small percentage of the community was recorded and low-abundance taxa may have been missed in some pools because they are less likely to be found than abundant taxa, thereby reducing their occupancy score. Such a sampling artefact may occur in

virtually all the field data sets that have been used to test abundance-occupancy relationships. However, the diagrams clearly show that some low-abundance taxa were recorded in many pools, indicating that my sampling methods, at least when combined over all four sampling periods, were sufficient to record consistently at least some of the low-abundance taxa.

The positive abundance-occupancy relationship tended towards a triangular shape, also found by Warren and Gaston (1997). Apart from one exception (the microcrustacean *Diaptomus gracalis* in the baited traps), the most abundant species occupied all patches. All relationships were highly significant and rank correlation coefficients were high. However, species which were low in abundance were variable in their occupancy and species which were high in occupancy were variable in their abundance. Therefore, high abundance is a good predictor of occupancy although low to moderate abundances appear more variable and occupancy in these taxa may be determined by a number of factors.

Several species of both active (e.g. chironomid larvae) and passive (e.g. microcrustacea and the Hydracarina) dispersers were present in all pools, over a range of abundances. Some species that are highly active dispersers, such as the adult Coleoptera, were never present in all patches although one species, *Dytiscus lapponicus*, was considerably more widespread than other Coleopteran species. This indicates that the dispersal ability of a taxon does not necessarily affect its position in the abundance-occupancy relationship.

Although measured body size data for individual species is not available, certain categories of body size are clear, e.g. the smallest group were the microcrustacea and the largest the diving beetles. The most abundant species in the

relationship appeared in all patches, in all but one case, and were the smallest body-sized group, the microcrustacea. This pattern was also observed by Gaston and Lawton (1988) in a study of insect populations, who found that common, widespread, widely fluctuating species tended to be small. However, being small does not imply being abundant and widespread; microcrustacean species were highly variable in both occupancy and mean abundance. Large-bodied taxa such as the Coleoptera, Odonata and Trichoptera were consistently low in abundance and generally tended to occupy less than half the patches. The largest body-sized taxa to appear in all patches were the three predatory chironomids. This is interesting when considering literature which reports that predators are rare (see review by Spencer, 2000) even when small (Ahlering & Carrel, 2001), although such reports generally refer to density and biomass without discussing distribution.. As a further point of interest, the two predatory microcrustacean species were moderately low in abundance, though high in occupancy. Low abundance taxa covered a range of body-sizes from microcrustacea to diving beetles. Although further investigation using measured body-size could reveal more specific patterns, these data do indicate that there is some pattern in distribution of body size in that large bodied species were not widespread or abundant. This was also found in the experimental microcosms of Holt *et al.* (2002) and concurs with the abundant literature documenting the rarity of large taxa. Another possible pattern that may benefit from further analysis is that of trophic level: predators were moderately low in abundance, but the smallest predators were widespread.

Niche breadth has been suggested as a possible mechanism for creating positive abundance-occupancy relationships (Brown, 1984). Species with a wider

niche breadth are able to occupy more patches in a heterogeneous habitat and will be more abundant within those patches as they can exploit a wider range of resources. Conversely, species with a narrow niche breadth will occupy fewer patches in a heterogeneous habitat and be more rare, as they are only able to exploit limited resources. The habitat-patch types in the system at Forsinard appear to be rather uniform within the pools, and similar between pools, yet there is still a positive relationship between abundance and occupancy. This is therefore a system in which Brown's (1984) niche-breadth mechanism seems unlikely to have a strong effect, suggesting that niche breadth is not a necessary mechanism.

Populations in the pools at Forsinard are quite possibly subject to the rescue effect, as discussed in Chapter 4, where immigration decreases the probability of a local population becoming extinct. It has been suggested that the rescue effect can result in positive abundance-occupancy relationships if the rate of immigration per patch increases as the proportion of patches occupied increases (Hanski, 1991b). Hanski states that the rescue effect hypothesis assumes that local abundance affects distribution and vice versa. The most abundant taxa in my pools were the most widespread although widespread taxa were not all the most abundant. However, it is possible that widespread distributions of many low-abundance species may be persisting due to the rescue effect preventing the extinction of these low populations and that other mechanisms are limiting abundance. Nee *et al.*'s (1991) carrying capacity hypothesis may not apply here as high occupancy in their model results from large populations; high occupancy taxa in my pools vary in abundance. However, as Nee *et al.* (1991) point out, population size depends on many biological

factors and extinction and colonisation rates may be influenced by factors other than population size alone.

When comparing species that differ morphologically and ecologically, patterns in abundance–occupancy relationships tend to be less distinct than when comparing similar species (Maurer, 1999). Separating taxa into similar groups may result in a number of positive relationships, each with a different slope. This would explain the range of abundance values at maximum occupancy in my pools. The pools here are quite impoverished and most taxonomic groups are few in species but the microcrustacea are the most speciose group and would probably be suitable for separate analysis.

Biological factors that may be involved in determining population size and/or extinction and colonisation rates are interspecific interactions, particularly predation. The only certain way of testing for the effects of interspecific interactions is by removing the species involved and this is difficult in a natural system. However, Holt *et al.* (2002) showed that multi-species microcosm communities had better defined abundance-occupancy relationships than single species communities, where there were no biotic interactions. It is reasonable to consider that biotic interactions such as predation and competition may limit or increase distribution and/or abundance in the Forsinard pools, thereby helping to define the shape of the abundance-occupancy relationship. A combination of the rescue effect and predation pressure could be responsible for maintaining the numerous low abundance-high occupancy taxa observed.

There has been no clear evidence that a single mechanism is responsible for all abundance-occupancy curves and it is probable that a number of processes may be

working in combination (Gaston *et al.*, 1997). Although it is more problematic to test for causality in a natural system, the rescue effect coupled with interspecific interactions and restrictions due to body size may all be contributing to the pattern of abundance and occupancy in this system.

5.4.2 Predator:prey ratios

Variation in the ratios of predators to prey across the pool-size gradient was higher when each sampling method was compared separately than when data from all sampling methods were combined. This was most likely due to one, or a combination of two, effects. Either the bias in each sampling method towards certain taxa will bias the ratios (unbaited activity trap have the lowest mean ratio) or a smaller sample number and therefore a smaller number of individuals being included in the calculations when methods were separated lead to higher variation in the ratios (sediment samples tended to contain fewer individuals than activity traps). Neither pool size nor number of taxa affected the ratios when methods were considered separately or were grouped, suggesting that variation in the proportion of predators and prey is not driven by abiotic spatial scale or numbers of taxa, in this system at least. This contrasts with the findings of Spencer *et al.* (1999) who found a positive relationship between the proportion of macroscopic predator species and both area and species richness (more species were collected from larger pools and the effects of the two variables could not, therefore, be separated) and to a certain extent with Warren and Gaston's (1992) relationship with species number. In this latter study, the relationship was due to the smallest communities tending to have fewer

predators; communities (number of taxa) were not as small at Forsinard as some included in Warren and Gaston's analyses.

The mean proportion of predator species across all pools is 33% which is similar to that found by Bilton (2001) and Warren and Gaston (1992) and is comparable with the proportion of predators in the whole data set (35%). There were never more predator species than prey in the Forsinard pools, which is consistent with findings by Warren and Gaston (1992) in their meta-analysis of several data sets. Although there was considerable variation in the ratios of predators to prey at Forsinard, the mean ratio across all habitat patches (0.49 ±0.1 SD) was slightly lower but roughly equal to the ratio of the total species pool (0.53). This indicates that predatory taxa are very slightly less widespread than non-predators but both groups were roughly equally distributed across patches. These results may also suggest that the overall species pool (i.e. that of the whole pool complex) may determine individual patch (pool) predator:prey ratios. This similarity of ratios between patches and the whole species pool is consistent with the findings of Jeffries (2002) in established ponds but not in newly dug experimental ponds. However in the established ponds, ratios appeared to increase with species richness whereas the new ponds showed little relationship with species number. The spread of the augmented species pool across the site was the cause of converging predator:prey ratios in Jeffries' (2002) manipulation experiment. Minimal dispersal constraints between the pools at Forsinard may allow for a similar mechanism to exist here. As there was little species turnover between the pools in this study, scale-invariant predator:prey ratios may be expected. At the level of this measure of community structure,

individual pools appear to be acting as 'random draws' from the species pool as a whole.

5.4.3 Community composition

After partialling out season as a covariable and fitting environmental variables to each data set, a large amount of variation remained unexplained. Some of this may be due to small sample size but the majority can probably be attributed to natural variability, which can be expected in community data such as this.

After the effects of season had been removed, a small but significant amount of variability could be explained by pool size and location within the complex. Pool size was the major axis of variation in all DCAs. Measures of pool size, particularly area and perimeter (which are obviously highly correlated), tended to be negatively correlated with distance from the centre of the complex (periferality). This is also shown by Belyea and Lancaster (2002). Area and perimeter generally explained more of the variability in the data than periferality and gave significant values of P more frequently, suggesting it is size, not location within the pool complex, that determines community composition. When variability explained by area was removed, periferality explained little of the remaining variability in most cases.

Species turnover between pools was minimal (often <2SD) but the maximum variation detected in detrended correspondence analysis tended to be correlated with measures of pool size and periferality. At least one measure of pool size was found to be significant, for all data sets, in the canonical correspondence analysis. Periferality was also significant but this is confounded by a negative correlation with the size gradients. Although perimeter and area are highly correlated, area

consistently described more of the variability in the data than perimeter. Depth also appeared to be important, independently of area, in explaining composition for activity trap data, particularly for the Dytiscid beetle assemblages in baited traps, where it was the only significant variable in the CCA. Mean depth was found to be marginally significant in a similar analysis of beetle assemblages (Fairchild *et al.*, 2000) although site age had a greater influence. The response of beetle assemblages to depth is likely to be related to the consequential increase in volume. Both adults and larvae of Dytiscidae are active predators of the water column and pool volume is likely to be important for their specific habitat requirements. An increase in available space allows for an increase in total prey biomass which in turn may allow for an increase in population sizes of Dytiscidae, an increase in diversity resulting from the addition of rare species, or a combination of both.

The division between the smallest pools and the largest pools was much more distinct in activity trap data than sediment samples, which can be attributed to the different taxa collected. Activity traps favoured mobile taxa, such as the microcrustacea and the diving beetles, which are easily able to exploit an increase in pool volume and total energy resources. If total primary productivity in the water column increases with volume, microcrustacean biomass (mostly herbivores with two predators) is likely to increase, allowing predators of the water column to increase in abundance and diversity.

The majority of taxa in the sediment samples were Chironomidae, mostly detritivorous taxa of the benthos with a more sedentary lifestyle. If the large quantities of humic substances which are found on the bottom surface provide an abundant food source, pool size and the subsequent increase in total nutrient

availability may not be the limiting factor in determining chironomid abundance and diversity. Chironomids may ultimately be limited by other mechanisms such as top-down effects of predation or by their dispersal and colonisation abilities across the complex. In this system, these mechanisms may have stronger effects than food availability and may be the limiting factors of chironomid abundance and diversity. However, dispersal constraints between pools are similar and predator:prey ratios appear to be independent of pool size or total number of taxa. If predation or colonisation are limiting factors of chironomid abundance and diversity, each appears to be too similar across pools to create detectable patterns in composition along a size or location gradient.

From plotting the sample scores in the ordination diagrams of the DCA (Figures 5.3, 5.8 and 5.10) there is clear community shift along the size gradient when comparing the smallest eleven pools to the largest eleven pools. This is seen in all data sets but is more defined in activity trap data (Figures 5.3 and 5.8). When considering the species scores of all data sets (Figures 5.4, 5.9 and 5.11), several taxa appeared towards the centre of the ordination diagram indicating they were present in all or many pools with no detectable pattern across any gradient. A few taxa, however, displayed their optimal distributions at either extreme of the pool size gradient. The community shift between small and large pools, observed in Figures 5.3, 5.8 and 5.10, is therefore due to only a small number of taxa which have their respective optimal distributions at the extremes of the size gradient, whilst most taxa are not responding to a change in pool size.

In activity traps, pool area was the most significant variable. In both baited and unbaited traps, with the exception of *Diaptomus gracalis, Dytiscus lapponicus*

and *Agabus arcticus* at the higher end of the area gradient, and *Chaoborus obscuripes*, *Coenagrion hastulatum*, Oligochaetae, and *Alonella excisa* at the lower end of the area gradient, all taxa occurring towards the extreme ends of the gradient were rare or occasional and were found in a maximum of five pools per data set. At both ends of the size spectrum, taxa ranged in body size from microcrustacea to large diving beetles indicating there is no relationship between species optima and body size in these data. Generally, species optima at the higher end of the size gradient had more extreme values than species optima at the low end of the gradient. Although the taxa occurring towards the extremes of the size gradients appear to be driving the community shift displayed in the ordination diagrams, this must be interpreted with care. Random sampling effects cannot be ruled out as the mechanism responsible for the placement of rare taxa. A taxon that appears in a similar position along a gradient in more than one trap type (e.g. in both baited and unbaited activity traps) is less likely to be placed due to chance and, therefore, may more reliably represent its true optimum, or close to it. This is a reasonable assumption for an abundant taxon although more caution should be applied when interpreting the optimum of a rare taxon.

Taxa that display similar optima in both baited and unbaited activity traps are, at the higher end of the area gradient, the microcrustacea *Diaphanosoma* sp., *Diaptomus gracalis*, and *Alona elegans,* the diving beetles *Dytiscus lapponicus* and *Agabus arcticus* and the larvae of the whirligig beetle *Gyrinus* sp. The damselfly *Coenagrion hastulatum*, the caddisfly *Phryganea bipunctata,* and the Harpacticoida (although this latter taxon was very rare in both types of trap) are represented at the lower end of the area gradient in both trap types. These results are likely to be

related to the different habitat preferences of the taxa. The diving beetles and *Gyrinus* larvae are active hunting predators of the water column and the microcrustacea all feed on phytoplankton in the water column; these taxa may be responding to an increase in pool volume, as discussed previously. *Coenagrion hastulatum* clings to marginal vegetation and the increased perimeter:area ratio of smaller pools may be an important factor in its distribution throughout the complex. *Phryganea bipunctata* shows ontogenetic shift in its feeding habits, from predation to detritivory, and is generally a bottom dweller. The mechanisms responsible for its apparent optimum in smaller pools are unclear.

In the sediment samples, the most significant predictors of variation in the data were all measures of pool size. The taxa with their respective optima at the higher end of the size gradients were all very rare except for larvae of the diving beetle *Agabus*, and the predatory caddisfly *Cyrnus flavidus*. At the lower ends, all but the biting midge *Culicoides impunctatus*, larvae of the diving beetle *Hydroporus*, and the phantom midge *Chaoborus obscuripes*, were rare. Of the taxa occurring at the high ends of the size gradients in sediment samples, the whirligig beetle *Gyrinus minutus* also appeared at high ends of the area gradient in activity traps whilst the caddisfly *Phryganea bipunctata* appeared at the low end of the area gradient in the activity traps. The diving beetle *Acilius sulcatus* also appeared at both the high and the low ends of the size gradient in different random selections of data in the unbaited activity traps. These species were very rare, rare, or occasional in the samples and their respective occurrences along the gradients may be due to chance. Of the taxa appearing at the low values of the gradients, *Chaoborus obscuripes,* the dragonfly *Sympetrum danae* and the water boatman *Callicorixa wollastoni* also

appeared at the low end of the area gradient in activity traps. The latter two species were rare. The dragonfly *Libellula quadrimaculata,* which appeared at the lower end of the size gradient in the sediment samples, appeared at the high end of the gradient in baited traps and the low end in the unbaited traps. This taxon was rare in all sample types and location along the gradients could, again, be due to chance.

There is a clear community shift along the size gradient in these pools. Which taxa are driving the shift should be interpreted with care because rare taxa are hard to find and recordings may not be representative of their true range. Abundant and frequently occurring taxa (or at least taxa that occur more than occasionally) that are found at the same end of the size gradient in different data sets can be interpreted with some confidence as their position in the ordination is less likely to be due to sampling effects. At the higher end of the pool area gradient in the ordinations, in both baited and unbaited activity traps, *Dytiscus lapponicus* and *Agabus arcticus* occurred in pools with moderate frequency, and *Diaptomus gracalis* was widespread. *Coenagrion hastulatum* occurred with moderate frequency and was positioned at the lower end of the pool area gradient in both activity trap types. In sediment samples, *Agabus* larvae and *Cyrnus flavidus* were frequent at the higher end of the area gradient and *Culicoides impunctatus* occurred frequently and was positioned at the lower end. Species scores tended to be more distal for the taxa at the higher ends of the gradients. Rare taxa appear at both ends of the size gradient in the ordination diagrams but sampling effects cannot be ruled out here.

The results of these analyses indicate that some measure of pool size is responsible for community shift in invertebrate assemblages of the bog pools at Forsinard. Rare taxa in the analyses may be emphasising this shift and this must be

interpreted with care. However, these results do suggest that it is the frequently occurring taxa which display their respective optimal distributions towards the extremes of the size gradient that are driving true community shift over the pool size gradient.

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6 Discussion

6.1 THESIS SUMMARY

This thesis characterises species richness and community structure over a habitat-patch size gradient of a typical bog-pool complex, investigating the effect of pool size on aquatic invertebrate communities. In this study, twenty-two pools were surveyed ranging in area from 8.6 m^2 to 280.9 m^2 within a single complex at Forsinard in the north of Scotland. Three different sampling methods were used: baited and unbaited activity traps and a sediment sampler, to collect a wide range of taxa. Sampling took place on four occasions between April and September 1999. Univariate and multivariate methods were used to investigate the effects of pool size and pool location within the complex on species richness and community composition. Predator:prey ratios were calculated across pool area and taxon richness gradients to determine any proportional changes in trophic levels. Abundance–occupancy curves were plotted to observe patterns in distribution and average density of each taxon across the study pools.

Sixty-nine different taxa were identified from the twenty-two study pools. Two IUCN British Red Data Book species were recorded: the Northern Damselfly, *Coenagrion hastulatum* (Charpentier), and the cased caddisfly, *Nemotaulius punctatolineatus* (Retzius). Three species of aquatic Coleoptera were collected that have Nationally Notable status according to Ball (1986): *Dytiscus lapponicus* Gyllenhal, *Ilybius aenescens* Thomson and *Gyrinus minutus* Fabricius. All these species are typical of, and often restricted to, this habitat type. The three different

sampling methods differed in their sampling efficiency and each gave a different species spectrum. A distinct seasonal change in the samples was also observed.

Generally, relationships between taxon density and pool area were weak or non-existent. However, the number of Dytiscidae diving beetle species collected in baited activity traps increased significantly with pool area. This suggests that Dytiscidae species richness does increase with pool size in this system. There was a significant positive relationship between total predator density and pool area which was attributed to the increase in diving beetle taxa only. No other taxonomic or trophic group showed a relationship between taxon density and pool size.

Although taxon density did not generally differ in this study, taxon assemblages were heterogeneous. Detrended Correspondence Analysis indicates that, although species turnover was minimal across the pool size gradient there was evidence of community shift between small and large pools. Multivariate techniques showed that pool area, depth and distance from the centre of the pool complex (periferality) all had small but significant effects on community composition, although periferality is confounded by a negative correlation with pool size. Between certain taxa there were distinctly different optima along the pool size gradient driving the significant shift in composition.

This shift was not reflected in predator:prey ratios. Ratios of the number of predator taxa to prey taxa for each pool ranged from 0.34 to 0.78 with a mean of 0.49 ± 0.1 SD but variability was not affected by pool area or total taxonomic richness.

Taxa displayed a positive relationship between occupancy and abundance although there was variability in the abundance of widespread taxa and in the

occupancy of rare taxa. Large bodied taxa tended to be less widespread and the most abundant taxa were small.

6.2 PATTERNS ACROSS THE POOL SIZE GRADIENT AND THE MECHANISMS INVOLVED

6.2.1 Pool size or pool location within the complex?

All other measured environmental gradients being similar, two gradients in this system might affect species composition: spatial distribution of the pools and pool size. Spatial distribution is related to the regional effect of dispersal ability. Once a species has colonised a pool, pool size may affect its establishment *via* local mechanisms such as availability of and competition for resources and/or differences in predation pressure from established taxa. In the multivariate analysis, distance from centre of the complex was the only measure of pool location to affect community composition and this was confounded by a negative correlation with pool size. In each analysis at least one measure of pool size, most frequently pool area, explained significantly more of the variation in the data than any measure of pool location, indicating that location within the complex is of secondary importance.

6.2.2 All taxa do not have the same response

In a recent study of a series of ponds within a 4 km radius (Rundle *et al.*, 2002), species richness and community dissimilarity in Coleopterans were related to pond permanence and maximum area whereas microcrustacean diversity was similar across all pools. The frequency of occurrence between sites was the same for both groups, despite major differences in their dispersal mechanisms. These are very similar results to those in this thesis, which showed an increase in Dytiscid diving

beetle taxon density with pool size but, overall, no relationship in the microcrustacea. Maximum depth, which is closely correlated with pool area in the Forsinard pools, was the only significant predictor of beetle composition. Frequency of occurrence was shown to differ in my study, however, with diving beetles being generally less widespread than microcrustacea, although this was probably related to body size rather than dispersal mechanism.

Differences between pools were generally more detectable in the baited traps. This can be attributed to changes in diving beetle assemblages, as indicated by an increase in their taxon density with pool size. Although there was no significant effect of pool area or taxon richness on predator:prey ratios, the positive relationship in baited traps between the proportion of predators and pool size approached significance. (The effect of an increase in diving beetle taxa on predator proportions may be diluted by the number of other taxa in the assemblages.) This trend is reflected in the ordination results which place many of the rare beetle taxa at the higher end of the pool size gradient in both baited and unbaited activity traps, although the position of individual rare taxa in ordination must be interpreted with care due to possible sampling error. Abundance-occupancy relationships confirm that the beetle taxa were not generally widespread. These results suggest that larger pools do support more beetle taxa than smaller pools due to the addition of rare species.

Although niche space is unlikely to become more diverse in larger pools, pool depth does increase with area and was shown to be the only significant factor determining composition in the beetle assemblages. This is possibly connected with an increase in total prey biomass with depth, allowing for an increased number of

predator individuals and a subsequent increase in number of beetle species. An increase in the depth of the water column appears to be the major factor determining diving beetle composition. The shift in beetle composition together with an increase in relative abundance of a small number of non-beetle taxa with pool area, and the occurrence of one or two rare taxa at the higher end of the size gradient appear to be the major factors determining community composition across the pool size gradient.

It is reasonable to assume that not all species respond in the same way and that only a small proportion of taxa are responsible for the majority of the variability in composition. Jeffries' (2003) investigation of incidence in pond invertebrates suggest that individual species show idiosyncratic responses to a number of determining factors, rather than most species responding in a similar way to one or two dominant influences. My results support these findings; only a few species appear to be showing a response to the change in pool size.

6.2.3 Differences between taxa from activity and sediment samples

Both richness and composition of taxa collected in activity traps showed more variation across the pool size gradient than taxa collected in sediment samples. Even with a bias in sample size (more samples were taken from larger pools) and the subsequent increase in number of individuals, there was still no relationship between number of taxa collected in sediment samples and pool size. Unbaited activity traps displayed a positive relationship when sample size was biased, which disappeared when sample number was standardised. Although species turnover was similar in activity traps and sediment samples, community shift over the size gradient was much less distinct in the sediment samples and correlated less well with the first axis

in DCA. Taxa in activity traps had more distinct optima towards the extremes of the size gradients than taxa in sediment samples. None of the taxa that displayed an optimum towards the higher or lower end of the size gradient were from the family Chironomidae, which were collected in abundance in the sediment samples and greatly determine composition in this sampling method. Chironomid taxon density and composition cannot be predicted by measures of pool size or abundance in this system.

6.2.4 Why chironomid taxa do not respond to pool size or number of individuals

Except for three predatory taxa, chironomid taxa were detritivores. Humic substances are abundant on the pool bottom and may be a non-limiting food resource for chironomids, even in the smallest of the study pools, thereby reducing competition. Limiting factors on chironomid diversity may be firstly, the dispersal ability to colonise a pool, secondly the chemical parameters of the aquatic environment and thirdly, predation pressure from the many large and active predatory taxa found in bog pools such as Dytiscidae, *Sialis lutaria, Cyrnus flavidus,* and larger instars of Phryganeidae. However, if one of or all these mechanisms are limiting factors, then the intensity of the limitation appears to be independent of pool size, thus there is no pattern in chironomid diversity across the pool size gradient. Dispersal constraints within the complex appear similar due to the close proximity of the pools to one another and water chemistry results showed little variation between pools. Similar predation pressure on chironomids is partly suggested by the similar predator:prey ratios across the pool size gradient. Although there were more predatory beetle species collected from larger pools in the baited traps, and more

beetle individuals in these traps when compared to unbaited traps and baited traps from smaller pools, there was no relationship between pool size and beetle density in unbaited traps. The increase in abundance of beetles collected in baited traps with pool size is likely to be due to individuals being attracted from an increasingly larger area rather than a real increase in density. This suggests a similar 'real' encounter rate in all pools and therefore similar predation pressure.

6.2.5 The importance of measuring community composition

Dissimilarities in community composition were identified across a pool size gradient that were not detected when measuring taxon density, despite the same data being used. This indicates that, even in standardised sampling units which sample only a small proportion of the assemblage, community composition and subsequently structure is more sensitive to pool size than taxon richness. Therefore, monitoring species diversity alone may not be the most appropriate way of identifying community variability caused by a habitat-patch size gradient and probably many other variables. A similar conclusion was reached by Summerville and Crist (2003) when determining lepidopteran community composition and species diversity in North American deciduous forests. Due to the difficulties in determining true species richness (Bunge & Fitzpatrick, 1993; Nichols *et al.*, 1998; Boulinier *et al.*, 1998; Gotelli & Colwell, 2001) many studies can produce only estimates of species richness or are actually measuring species richness per standardised sampling unit, i.e. species density. In these types of studies especially, it is important that composition, not just number of species, is investigated if true community response is to be determined. These results indicate that in systems where it is not possible to

exhaustively sample or identify all species, it is still possible to detect, using multivariate techniques, dissimilarities in community composition and response to measured variables.

6.3 UNIFYING FACTORS ACROSS THE POOL COMPLEX

Similar determining environmental variables such as water chemistry, altitude, climate and microhabitat diversity between pools should, in theory, allow the same species to colonise and become established in all pools. However, pool area differs by over an order of magnitude across the study pools. In accordance with island biogeography theory (MacArthur & Wilson, 1967), this should result in an increase in species richness with pool size. Except in one group of taxa, pools did not generally differ in the number of taxa found per standardised sampling unit, despite the difference in area. Ordination techniques provided evidence of some variability in composition due to different relative abundances across the size gradient for a small number of taxa. However, the relative abundance for many taxa was similar in all, or many, of the sampled pools regardless of size. Additionally predator:prey ratios did not differ significantly with pool area.

There is clearly some mechanism responsible for the convergence of taxon density and composition across the pool size gradient for the greater part of the species assemblages. The nature of this mechanism is interesting as island biogeography theory (MacArthur & Wilson, 1967) predicts that smaller pools should contain fewer species due to the effects of reduced immigration and increased extinction rates.

6.3.1 The rescue effect

It is of course possible that more extensive sampling would reveal a relationship with pool size but, except for diving beetle species, relationships did not even approach statistical significance in standardised sampling. This suggests that even if a relationship does exist, it is less well defined than island biogeography theory might predict. However, the theory also discusses the effect of isolation from the source species pool where an increase in isolation results in reduced colonisation rates and therefore fewer species. This may be the key to understanding why the Forsinard pools show only weak or non-existent patterns for the majority of taxa. It is hard to determine where or indeed what, the source species pool actually is when considering the whole complex but, all pools will be similarly isolated. Within the complex, pools are similarly isolated from each other and 'stepping stone' colonisation can take place (MacArthur & Wilson, 1967) enabling species to establish throughout the complex. A population may become extinct, or nearly so, due to stochastic or deterministic mechanisms and stepping stone recolonisation might then ensure the persistence of that population. This is effectively the rescue effect (Brown & Kodric-Brown, 1977) where small or fragile populations are continuously 'rescued' by colonisation from nearby populations. Each population does not therefore need to be independently viable to persist.

6.3.2 A single community?

Because there are many pools within the complex (641 in total) and they are close together in space, vulnerable populations are likely to be rescued or enhanced by immigrants from multiple neighbouring populations. Stable populations are also

likely to receive immigrants from several neighbouring populations. Gene flow between pools is thus likely to be high and thus the whole pool complex is likely to be responding as a single community, rather than as a number of sub-communities within a 'metacommunity'. There is likely to be a gradient in natural systems between single communities, albeit apparently separated into discrete habitat patches, and completely isolated habitat 'islands'. 'Metacommunities' consisting of metapopulations will exist somewhere between these two extremes. I propose that, due to similar mechanisms operating in all pools and the high connectivity between them, pools in complexes such as this are very close to, if not at, the single-community end of the gradient. However, given the wide range of dispersal abilities, diets, behaviour and other aspects of autecology displayed by the taxa in my study, it is quite possible that some taxa exist at different positions along this gradient. Hence some taxa, e.g. the microcrustacea, may be closer to existing as metapopulations than others.

6.4 CONCLUSIONS

Pool size has a small but significant effect on community composition which can mostly be attributed to an increase in beetle taxon density with pool area and an increase in the relative abundances of a small number of non-beetle taxa with pool size. The similarities in predator:prey ratios over the pool complex, taxon density of non-beetle taxa and the relative abundances over the size gradient of the majority of taxa are most likely due to similarity of the environmental variables between pools and minimal dispersal constraints allowing vulnerable populations to persist *via* the rescue effect, even in small pools. The rescue effect is probably so strong in this

system, due to the close proximity of the pools in space and minimal dispersal constraints, that the whole complex is responding as a single community consisting of several hundred inter-connected, similar habitat-patches.

These results show that habitat-patch or pool size is of small, but significant, consequence when considering the community dynamics of a system such as this, and that, except for a small number of mostly predatory taxa, small pools can sustain populations of many taxa from a regional species pool providing they are part of a series of highly inter-connected habitat patches.

6.5 REFERENCES

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Appendices

Appendix 4.1. Results of regression analysis for the effect of the log of pool area on the log of taxon density in sediment samples. Summary results are shown from ten random combinations of 1 sample per pool for each month. Maximum R^2, range of slopes, P, and degrees of freedom (DF) are shown.

	Max R^2	Slope	Min P	DF
All Taxa				
April	0.00	-0.033 - +0.012	0.34	21
June	0.00	-0.371 - +0.020	0.59	21
July	0.00	-0.044 - +0.026	0.72	20
Sept	0.02	-0.138 - +0.088	0.25	20
Chironomids				
April	0.05	-0.020 - +0.034	0.16	21
June	0.00	-0.043 - +0.372	0.34	21
July	0.00	-0.033 - +0.004	0.79	20
Sept	0.03	-0.037 - +0.147	0.22	20
Predators				
April	0.02	-0.092 - +0.062	0.24	21
June	0.06	-0.139 - -0.025	0.15	21
July	0.00	-0.060 - +0.029	0.54	20
Sept	0.00	-0.100 - +0.008	0.33	20

Appendix 4.2. Results of regression analysis for the effect of the log of pool area on the log of the number of a) all taxa, b) chironomid taxa and c) predatory taxa found in sediment samples. Each random selection consists of 1 sample per poo1 per season (4 seasons so 4 samples in total per pool). Cumulative numbers of taxa per pool are calculated from the 4 samples. R2 values, slope and P values are presented. Degrees of freedom = 19.

Random selection number	**R^2**	**Slope**	**P**
a) All taxa			
1	0.00	1.011	0.73
2	0.00	-0.010	0.69
3	0.00	-0.038	0.32
4	0.00	0.007	0.86
5	0.04	-0.058	0.21
6	0.00	0.006	0.82
7	0.00	-0.024	0.50
8	0.00	-0.035	0.37
9	0.00	-0.029	0.47
10	0.00	-0.010	0.75
b) Chironomidae			
1	0.00	0.002	0.93
2	0.00	-0.012	0.51
3	0.00	-0.014	0.57
4	0.00	-0.013	0.67
5	0.00	-0.014	0.60
6	0.00	0.012	0.54
7	0.00	0.005	0.76
8	0.00	0.003	0.90
9	0.00	-0.009	0.68
10	0.00	-0.020	0.38
c) Predators			
1	0.03	-0.125	0.21
2	0.00	-0.046	0.64
3	0.00	-0.094	0.36
4	0.00	-0.013	0.89
5	0.03	-0.127	0.22
6	0.07	-0.115	0.14
7	0.02	-0.119	0.25
8	0.05	-0.122	0.18
9	0.09	-0.093	0.29
10	0.00	-0.075	0.36

Appendix 5.1. Species codes for activity traps.

Code	Taxon
Ac cu	*Acantholeberis curvirostris*
Ac ha	*Acroperus harpae*
Ac su	*Acilius sulcatus*
Ac ve	*Acanthocyclops vernalis*
Ae ju	*Aeshna juncea*
Ag ar	*Agabus arcticus*
Ag la	*Agabus* larvae
Ag ob	*Agrypnia obseleta*
Al af	*Alona affinis/quadrangularis*
Al el	*Alona elegans*
Al elo	*Alonopsis elongata*
Al ex	*Alona excisa*
Al gu	*Alona guttata*
Al na	*Alonella nana*
Al ru	*Alona rustica*
Bo co	*Bosmina coregoni*
Ca wo	*Callicorixa wollastoni*
Ce se	*Ceriodaphnia setosa*
Ch ob	*Chaoborus obscuripes*
Ch sp	*Chydorus sphaericus*
Chir	*Chironomidae*
Co fu	*Colymbetes fuscus*
Co ha	*Coenagrion hastulatum*
Cu im	*Culicoides impunctatus*
Cy fl	*Cyrnus flavidus*
Di gr	*Diaptomus gracilis*
Diap	*Diaphanosoma* sp.
Dr de	*Drepanothrix dentata*
Dy la	*Dytiscus* larvae
Dy lap	*Dytiscus lapponicus*
Dy ma	*Dytiscus marginalis*
Dy se	*Dytiscus semisulcatus*
Gr te	*Graptoleberis testudinaria*
Gy la	*Gyrinus* larvae
Gy mi	*Gyrinus minutus*
Harp	*Harpacticoida*
He ca	*Hesperocorixa castanea*
Hy er	*Hydroporus erythrocephalus*
Hydr	*Hydracarina*
Il ae	*Ilybius aenescens*
Il gu	*Ilybius guttiger*
Il la	*Ilybius* larvae
Il so	*Ilyocryptus sordius*
La se	*Latona setifera*
Le ve	*Leptophlebia vespertina*
Li qu	*Libellula quadrimaculata*
Ly st	*Lymnephilus stigma*
Newt	Newt/Tadpole
Olig	*Oligochaetae*
Para	*Paracyclops* sp.
Ph bi	*Phryganea bipunctata*
Po pe	*Polyphemus pediculus*
Rh su	*Rhantus suturellus*
Si la	*Sigara* larvae
Si lu	*Sialis lutaria*
Si sc	*Sigara scotti*
Sy da	*Sympetrum danae*

Appendix 5.2. Species codes for sediment samples.

Code	Taxon name
Abla	*Ablabesmyia* sp.
Ac su	*Acilius sulcatus*
Acam	*Acamptocladius* sp.
Ag la	*Agabus* larvae
Ag ob	*Agrypnia obseleta*
Ca wo	*Callicorixa wollastoni*
Ch ob	*Chaoborus obscuripes*
Cmus	*Chironomus* sp./*Einfeldia* species group C
Co ha	*Coenagrion hastulatum*
Cory	*Corynoneura* sp.
Cu im	*Culicoides impunctatus*
Cy fl	*Cyrnus flavidus*
Dicr	*Dicrotendipes* sp.
Gl pr	*Glaenocorixa propinqua*
Gy mi	*Gyrinus minutus*
Hy la	*Hydroporus* larvae
Il ae	*Ilybius aenescens*
Il la	*Ilybius* larvae
Le ve	*Leptophlebia vespertina*
Li qu	*Libellula quadrimaculata*
Macr	*Macropelopia* sp.
Micr	*Microtendipes* sp.
Page	*Pagestiella* sp.
Ph bi	*Phryganea bipunctata*
Poly	*Polypedilum* sp.
Proc	*Procladius* sp.
PseA	*Psectrocladius* A
PseB	*Psectrocladius* B
PseC	*Psectrocladius* C
Serg	*Sergentia* sp.
Si la	*Sigara* larvae
Si lu	*Sialis lutaria*
Si sc	*Sigara scotti*
Sy da	*Sympetrum danae*
Tany	*Tanytarsus* sp.